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As the Nation's principal conservation agency, the Department of the Interior has basic responsibilities for water, fish, wildlife, mineral, land, park, and recreational resources. Indian and Territorial affairs are other major concerns of America's "Department of Natural Resources."

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THE FEEDING HABITS OF THE GREEN CRAB, *CARCINUS MAENAS* (L.)

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ABSTRACT

Green crabs are believed to be the cause of a decline during the 1940's in the commercial landings of the soft-shell clam (*Mya arenaria* L.). Collections of 3,979 green crabs from Plum Island Sound, Mass., and vicinity in 1954–56 provided the stomachs for a study of their feeding habits. Laboratory and field observations were also made. The green crab is an omnivore, but usually contains pelecypods. It uses its claws for both digging and feeding. Accessory organs other than eyes aid in directing it to food. Feeding is influenced by the abundance, size, and kind of food. Although all sizes of green crabs contained essentially the same kinds of food, pelecypods were most frequent in crabs with carapace widths of 30 to 59 mm. Most crabs apparently feed during the night; crabs with food in their stomachs were most numerous in catches made just after sunrise. Water temperatures of 7° C. and below reduced activity and presumably feeding as well. Low salinities, however, apparently did not affect feeding. Because female crabs were relatively more numerous than males in the fall, the season when newly settled juvenile *Mya* occur in abundance, they probably were more destructive than males in Plum Island Sound.

The New England landings of soft-shell clams, *Mya arenaria* L., declined from a high of 14.7 million pounds in 1938 (Fiedler, 1940) to a low of 2.3 million pounds in 1959 (Power, 1961). The decline seriously affected the fishery and stimulated action to determine the cause. In 1948, Congress authorized the Bureau of Commercial Fisheries to study the resource (Glude, 1955).

The research of the Bureau has resulted in many publications on the biology of the soft-shell clam, with especial attention being paid to the predators of the clam. Some of the studies included observations on mortality (Smith, 1950), population size (Spear, 1953), activity (Baptist, 1955; Smith, 1955), and parasites (Uzmann, 1952; Uzmann and Stickney, 1954; Stunkard and Uzmann, 1958; Stunkard, 1960). The effects of man (Glud, 1951; Glude, 1954) and other predators (Smith and Chin, 1953) on the fishery were also observed. Animal predators were eventually identified as the most probable cause of the decline in clams; many species are known to feed on soft-shell clams. For example, soft-shell clams are sometimes included in the diet of rock crabs, *Cancer irroratus* (Mead and Barnes, 1904); lady crabs, *Ovalipes occelatus*, and blue crabs, *Callinectes sapidus* (Belding, 1930); horseshoe crabs, *Limulus polyphemus* (Belding, 1930; Turner, 1949; Smith and Chin, 1953); moon snails, *Polinices duplicatus* (Sawyer, 1950; Hanks, 1952, 1957); winter flounders, *Pseudopleuronectes americanus* (Medcof and MacPhail, 1952); herring gulls, *Larus argentatus* (Mendall, 1934; Medcof, 1949); and black ducks, *Anas rubripes* (Mendall, 1949). None of these animals, however, seemed to be responsible for the low abundance of clams. Neither blue crabs nor lady crabs are common north of Cape Cod, and none were found on the clam flats. The other predators either fed infrequently on clams or were found in only some of the areas where clams were not abundant.

One other possible predator, the green crab, *Carcinus maenas* (L.), was widespread, abundant, and apparently a species that had recently extended its range north of Cape Cod. Scattergood (1952) documented the spread of the green crabs from south

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of Cape Cod during the late 1800's to northern New England in the 1940's and 1950's. By 1954, green crabs had extended their range northeastward to Wedgeport, Nova Scotia, Canada, and were also very numerous in Massachusetts, New Hampshire, and Maine. Glude (1955) and Taylor, Bigelow, and Graham (1957) considered an increase in air and surface sea-water temperatures north of Cape Cod to be an important factor in the increase in abundance and extension of the green crab's range.

The green crab was reported to be the most probable cause of the decline in soft-shell clams by Smith and Chin (1953), Glude (1955), Medcof and Dickie (1955), and Smith, Baptist, and Chin (1955). MacPhail, Lord, and Dickie (1955) and Dearborn[1] observed the feeding of green crabs in laboratories where they were restricted to certain foods, but only a few observations were available on the feeding of green crabs in nature. Smith and Chin (1953) first reported a green crab actually feeding on a soft-shell clam that it had apparently just dug out of the sediments. Hence, a study to determine feeding habits under natural conditions was needed for a broader understanding of the impact of this predator on its environment, and particularly on the soft-shell clam.

I studied the feeding habits of green crabs while at the field stations of the Bureau of Commercial Fisheries in Newburyport, Mass., and in the Narragansett Marine Laboratory, University of Rhode Island, Kingston, R.I., from 1954 through 1956. The stomach contents of green crabs collected from Plum Island Sound, Mass., and Hampton Harbor, N.H., were examined to determine the relative importance of their foods; I also made some observations on the relation of feeding behavior to the environment.

MATERIALS AND METHODS

Green crabs occurred and were collected in two distinct zones at low tide—the upper intertidal zone and the shallow subtidal zone. Crabs were caught at the edges of salt marshes in Plum Island Sound, Mass., and Hampton Harbor, N.H. (fig. 1), by opening caves in the banks of cordgrass (*Spartina*) and searching through seaweeds at the upper edges of the banks and beneath sods that had fallen onto the clam flats (table 1). Crabs were collected from the subtidal zone by dragging a scallop dredge at the edges of channels in Plum Island Sound, Mass. (table 2). The net was 76.2 cm. wide and 20.3 cm. high at the mouth and had a 51-mm. mesh (stretched measure) netting bag 76.2 cm. deep. A weighted line at the leading edge of the net scraped over the bottom; probably crabs buried in the sediments were missed, and active crabs were most likely to be captured. All dredge

TABLE 1.—*Number of green crabs dug from the banks at Plum Island Sound, Mass., and at Hampton Harbor, N.H., 1954–55*

Hales Cove		Bluff Creek		Hampton Harbor	
Date	Crabs	Date	Crabs	Date	Crabs
1954	*Number*	*1954*	*Number*	*1954*	*Number*
Sept. 23	51	Oct. 5	50	Sept. 16	35
Oct. 22	11	Nov. 2	93	Oct. 19	72
Nov. 5	96	Dec. 8	45	Nov. 18	113
Dec. 6	72			Dec. 22	155
1955		*1955*		*1955*	
Jan. 12	27	Apr. 18	83	Jan. 27	44
May 19	36	July 23	49	Feb. 16	83
Aug. 26	8	Oct. 21	137		
Oct. 21	13	Nov. 23	50		

TABLE 2.—*Number of green crabs dredged from the subtidal zone at Plum Island Sound, Mass., 1954–56*

Plum Island River		Lufkins Flat	
Date	Crabs	Date	Crabs
1954	*Number*	*1954*	*Number*
Oct. 5	[1] 24	Oct. 5	59
Oct. 28	10	Nov. 2	60
Nov. 5	62		
1955		*1955*	
Apr. 18	20	Apr. 18	20
May 26	47	May 18	33
June 13	54	June 13	37
July 18	55	July 18	57
Aug. 15	64	Aug. 15	51
Sept. 10	52	Sept. 10	128
Sept. 23	68	Sept. 23	44
Oct. 9	54	Oct. 9	67
Oct. 21	74	Oct. 21	44
Nov. 7	49	Nov. 7	69
Nov. 23	0	Nov. 23	0
1956		*1956*	
May 11	2	May 11	58
June 11	40	June 11	48
June 11	22	June 11	16
July 23	27	July 23	59
July 23	27	July 23	46
Aug. 6	25	Aug. 6	49
Aug. 6	27	Aug. 6	43
Sept. 4	10	Sept. 4	52
Sept. 5	67	Sept. 5	54
Sept. 21	26	Sept. 21	44
Sept. 22	51	Sept. 22	46
Oct. 5	62	Oct. 5	49
Oct. 19	57	Oct. 5	42
Oct. 20	61	Oct. 19	53
Nov. 5	24	Oct. 20	98
		Nov. 5	71

[1] Two crabs not used for stomach analysis.

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[1] Dearborn, John H. 1957. A preliminary study of the food habits of the green crab, *Carcinides maenas* (L.) with particular reference to the soft-shell clam, *Mya arenaria* L. M.S. thesis, Mich. State Univ. Agr. Appl. Sci., 48 pp.

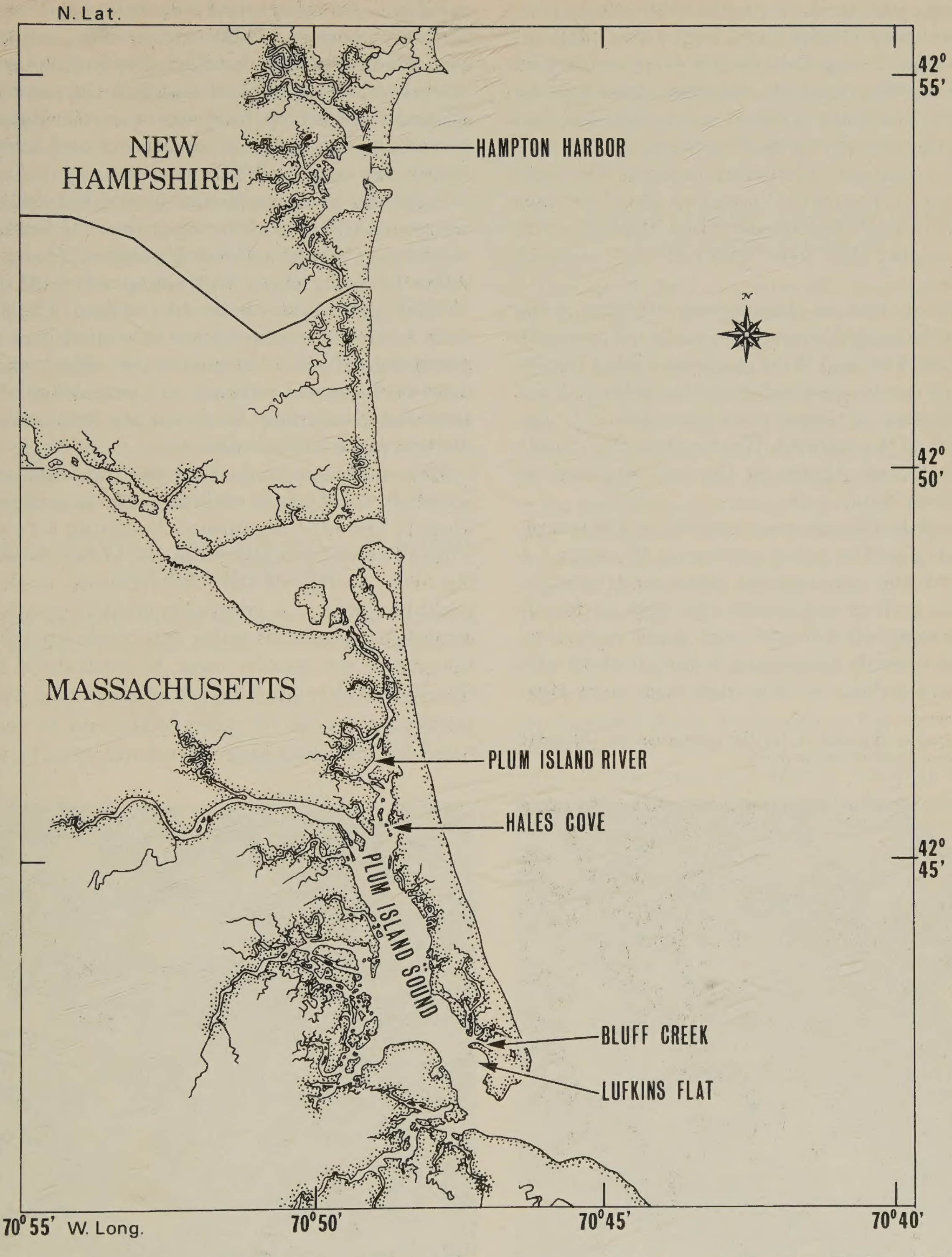
N. Lat.
NEW HAMPSHIRE
HAMPTON HARBOR
MASSACHUSETTS
PLUM ISLAND RIVER
HALES COVE
PLUM ISLAND SOUND
BLUFF CREEK
LUFKINS FLAT
N
42° 55'
42° 50'
42° 45'
70° 55' W. Long.
70° 50'
70° 45'
70° 40'

FIGURE 1.—Areas sampled for green crabs in Plum Island Sound, Mass., and Hampton Harbor, N.H.

collections were made during the ebb tide just before low water. Observations with a face plate indicated that during the ebb tide green crabs were actively moving from the intertidal zone into the channels. The crabs taken at nearly low tide had had an opportunity to feed in the intertidal zone during a complete tide before capture. The sample size was arbitrarily limited to about 50 crabs or eight drags. Occasionally more than 50 crabs were caught; all were retained for stomach analysis.

Tables of data on the stomach contents of the green crabs caught during this study are available in the U.S. Fish and Wildlife Service Data Report 29, which can be obtained from the Branch of Reports, Bureau of Commercial Fisheries, U.S. Department of the Interior, Washington, D.C. 20240. The tables and figures in the text are derived from these data.

Each crab stomach was removed at the laboratory and placed in a vial containing Formalin.[2] A record of the sex, molting stage, and carapace width, as well as the presence of eggs on female crabs, was included in each vial. Later each stomach was opened, the contents were flushed with water into a dish, and the food items were separated and identified under a dissecting microscope. The occurrence and, whenever possible, a count of each food item were recorded. For each collection of crabs, the total of these data and the number of stomachs containing food were used to obtain the percentage frequency of occurrence and average number of each food item per crab.

Estimates of the amount of food in the stomachs were separated into three categories: (1) stomachs containing tissues and hard parts of foods, (2) stomachs nearly empty, containing only hard parts of foods, and (3) stomachs with no food. The stomachs in the first category are tabulated here as a percentage of all crabs caught per collection, and those in the second category as a percentage of the stomachs containing food. Empty stomachs are omitted from all calculations.

Most food consisted of crushed or fragmented remains; so, I used various hard structures to identify the food organisms. Assigning a food to a definite species category was not always possible, but often enough of the food remained so that I could assign it to a general taxonomic group. As a consequence, not all major taxonomic groups are the sum of the specific items. Mollusk shells were the most readily identified food items (fig. 2). In particular, species of pelecypods could be recognized because their hinge structures usually were

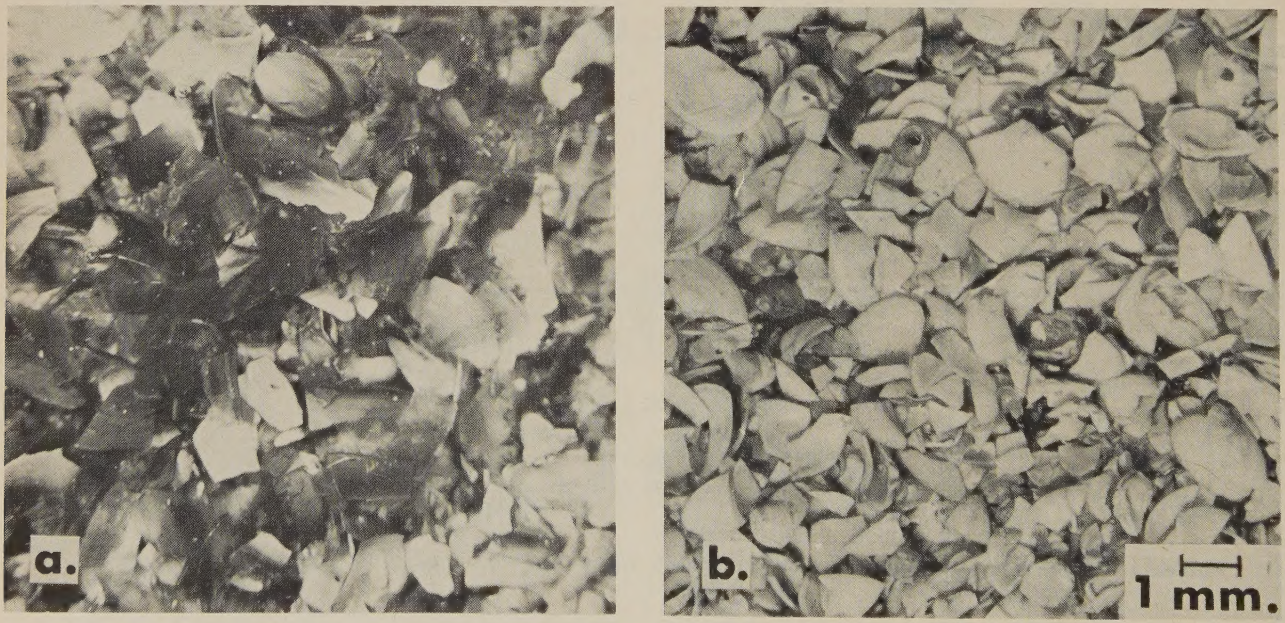

FIGURE 2.—Mollusk foods from the stomachs of green crabs: a. *Mytilus edulis*, and b. *Gemma gemma* and *Hydrobia minuta* (1-mm. scale near lower edge of figure).

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[2] Trade names referred to in this publication do not imply endorsement of commercial products.

intact. Because of their frequent occurrence in the stomachs, the species *Mya arenaria*, *Gemma gemma*, and *Mytilus edulis* were separated in the analyses; other species of pelecypods were combined. Gastropods were identified from the shells, operculi, and sometimes the radulae. Annelids were identified by their jaws (whole worms were rarely found). Arthropods could rarely be identified to species but were separated into three general groups: (1) crabs—the heavy, pigmented exoskeletons of green crabs, rock crabs, and horseshoe crabs; (2) small arthropods—the light, translucent exoskeletons of amphipods, isopods, and small shrimp; and (3) barnacles (shells and bodies). Insects, fish remains (mostly bones), Foraminifera, and colonial hydroids were also found. Only two plant foods, algae and cordgrass (*Spartina*), were identified. Many stomachs contained food remains that were classified as unidentified tissues.

THE RELATIVE FREQUENCY OF FOODS IN GREEN CRABS

Mya was only 1 of 31 kinds of food identified in the stomach contents during this study (table 3).

TABLE 3.—*List of organisms in the stomachs of 3,979 green crabs collected in 1954–56*

- Annelids
  - *Nereis* sp.
  - *Glycera* sp.
  - *Clymenella* sp.
- Mollusks
  - Pelecypods
    - *Solemya velum*
    - *Mytilus edulis*
    - *Modiolus demissus*
    - *Mysella planulata*
    - *Gemma gemma*
    - *Petricola pholadiformis*
    - *Tellina* sp.
    - *Macoma* sp.
    - *Ensis directus*
    - *Mya arenaria*
  - Gastropods
    - *Littorina* sp.
    - *Polinices* sp.
    - *Odostomia* sp.
    - *Hydrobia minuta*
- Arthropods
  - Crabs
    - *Pagurus* sp.
    - *Cancer irroratus*
    - *Carcinus maenas*
    - *Limulus polyphemus*
  - Small arthropods
    - Isopods
    - Amphipods
    - Natantia
  - Barnacles
    - *Balanus* sp.
- Other animals
  - Foraminifera
  - Colonial hydroids
  - Insects
  - Fish
- Plants
  - Algae
  - *Spartina* sp.

Both animal and plant foods occurred in the stomachs, but not with equal frequency (fig. 3); only one-third of the 3,979 stomachs with food contained plants, whereas 88 percent contained animals. Mollusks, and especially pelecypods, were the most frequent animal foods in the stomachs, and *Mytilus* was the most frequent species. *Mya*, *Gemma*, and other pelecypods occurred in about one-fourth of the stomachs. Only the plant food *Spartina* was found in as many stomachs as some of the pelecypod species. Remains of large arthropods and fish, probable indicators of cannibalistic and scavenging food habits, respectively, were in few stomachs; obviously green crabs are essentially omnivorous.

THE FEEDING CAPABILITIES OF GREEN CRABS

Certain items in the stomachs and observations of feeding in the laboratory provided information on the food-gathering capabilities of green crabs. A few stomachs contained the bodies and thoroughly crushed shells of barnacles. The presence of mussels with the barnacles in some stomachs suggested that one food was eaten incidentally to the other. In the laboratory, however, green crabs ate barnacles alone; they used their chelae to tear individual barnacles from clusters adhering to wood and glass. The eating of barnacles, thus, was not necessarily contingent upon the ingestion of another food. Occasionally a stomach contained gastropod meats, identified by the presence of a radula but no shell fragments. Green crabs were not seen eating gastropods in the laboratory, but perhaps the snails were eaten in the same fashion as *Mya*. The crabs usually exposed the meats of *Mya* 10 mm. long or longer by crushing or chipping off pieces of the shell with the chelae. Then they easily severed the adductor muscles, tore out pieces of meat, and ate them. Only the largest clams resisted attacks by green crabs. MacPhail et al. (1955) and Dearborn[3] found that *Mya* with shells equal in length or shorter than the width of the carapace of a green crab were successfully broken into and devoured. In the laboratory, I saw clams shorter than 10 mm. picked up, crushed by the chelae, and then ingested nearly whole. Many nearly intact valves were found in the stomachs—some in crabs as small as 10 to 19 mm. These results suggested that green crabs probably ate whole animals more frequently than Dearborn believed. Crescent-shaped pieces of *Spartina* were sometimes found in green crab stomachs. In the laboratory green crabs ate the stems of *Spartina* by holding them in their chelae so that the mouthparts surrounded one end. Dow and Wallace (1952) provided additional observations on the

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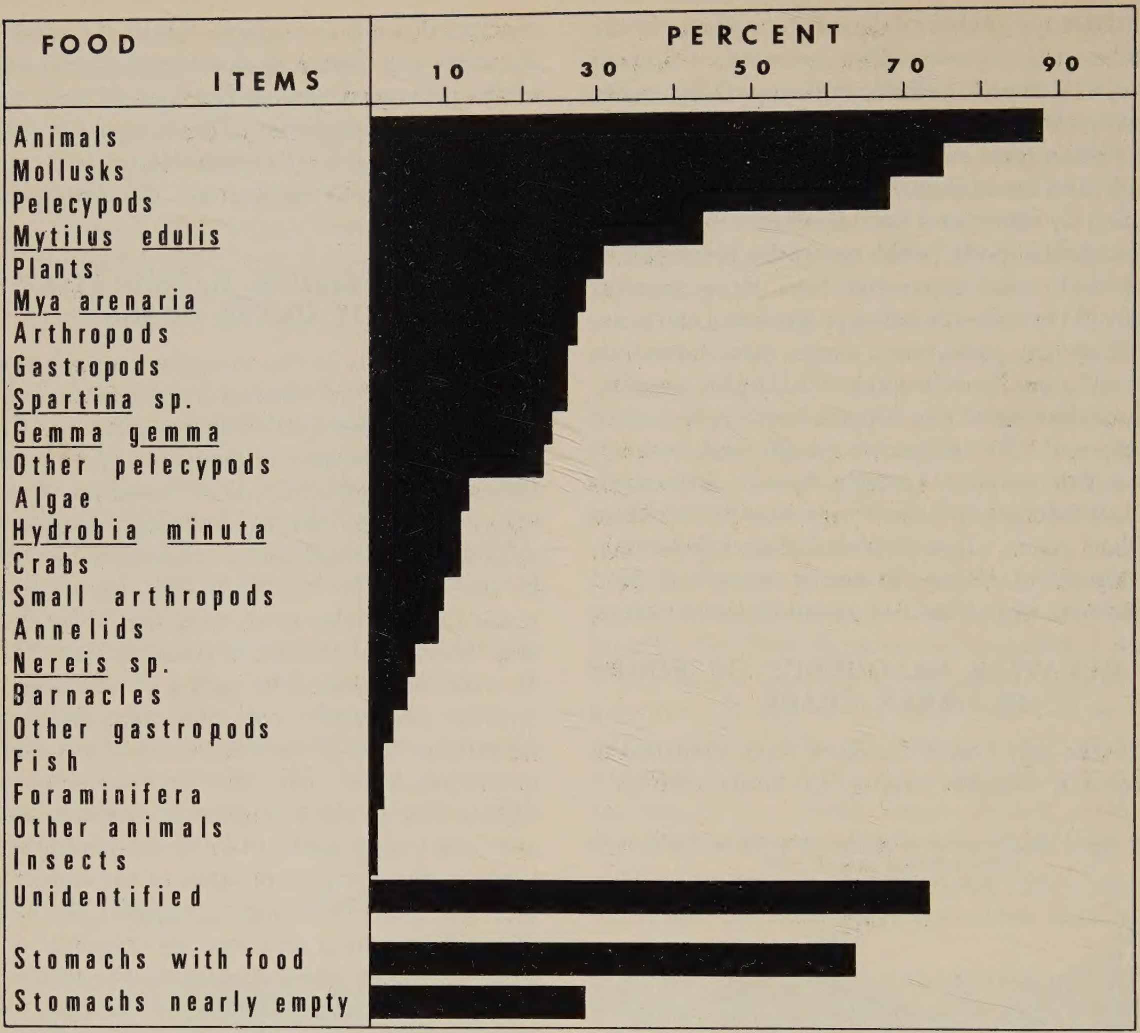
[3] Footnote 1.



FOOD ITEMS	AVERAGE NUMBER
Mollusks	13.9
Pelecypods	9.4
Gastropods	4.6
Hydrobia minuta	4.1
Mytilus edulis	4.1
Gemma gemma	3.1
Mya arenaria	1.2
Other pelecypods	1.0
Other gastropods	.1
Annelids	.06
Nereis sp.	.06
Other annelids	.004
TOTAL NO. of CRABS	3,979

FIGURE 3.—The relative importance of foods, analyzed by the percentage frequency of occurrence per sample of crabs and by the average numbers of certain animals per stomach, in the stomachs of 3,979 green crabs collected in 1954–56.

use of chelae by green crabs, and Borradaile, Potts, Eastham, and Saunders (1958) described the holding, severing, and chewing action of the green crab's mouthparts.

Carthy (1958) discussed accessory sense organs other than eyes which may help to direct green crabs to food. I observed how the chemical senses arouse green crabs in the laboratory. Ten crabs, from which the eye stalks had been removed, were held in an aquarium where 54 *Mya* lived in the sand. During 18 days of observation, all the crabs remained buried in the sand and did not search for the clams. On the 18th day, when juice of the quahog (*Mercenaria mercenaria*) was poured into the aquarium, the crabs almost immediately rose out of the sand and moved about, as if in search of food. Such an unoriented reflex action of the whole animal or kinesis to chemical stimuli was discussed by Allee, Emerson, Park, Park, and Schmidt (1949).

Abundance of certain foods undoubtedly affects predation by green crabs and is interrelated with their food-getting capabilities. Bottom samples taken in 1954 by Smith (1955) from areas protected from crabs by Saran screening had more *Mya* per square foot at Hales Cove than at Hampton Harbor. During the same year, more crabs contained *Mya* at Hales Cove than at Hampton Harbor. Thus, the crabs at Hales Cove reacted to the greater relative abundance of *Mya* by eating more of them.

Small animals were most numerous in the stomachs. Many crabs consumed large numbers of such small mollusks as *Gemma* and *Hydrobia* (table 4). Some pelecypods were ingested soon after setting, when they were very small. Smith (1955) observed that clams 2 to 12 mm. long were most abundant at Hales Cove in September and October and deduced that this phenomenon was probably an annual event. *Mya* occurred most frequently in green crab stomachs during September to November.

Some foods were eaten frequently by certain groups of crabs. *Spartina* was found most often in intertidal crabs (fig. 4), although crabs from both the intertidal and subtidal zones usually contained more animals than plants. Plant foods, especially *Spartina*, were abundant near the caves inhabited by green crabs and on islands that were relatively near the subtidal zone. Subtidal crabs contained animal foods, apparently from the clam flats, rather than *Spartina*.

TABLE 4.—*Numbers of certain organisms in selected specimens of green crabs*

Width of crab	Sex[1]	Food					
		Mytilus	*Gemma*	*Mya*	Other pelecypods	*Hydrobia*	Other food (not counted)
Mm.		*Number*	*Number*	*Number*	*Number*	*Number*	
43	M		165	2		18	None
48	M		181	1		50	Algae and *Spartina*
48	F		123	4		92	Algae
52	F		23			355	None
53	F		17			382	*Spartina*
49	F		18			309	None
44	F	159			1		Algae and *Spartina*
58	F	236		3	2		Foraminifera and *Spartina*
53	F	120		7	2		None
57[2]	M	32		35	17		Crabs, algae, and *Spartina*
65	F	24		48	74		Algae and *Spartina*
32	F	48		22			Crabs, algae, and *Spartina*
42	F	6		83	7		Small arthropods and *Spartina*

[1] M=male; F=female.

[2] The stomach of the crab also contained one *Nereis*.

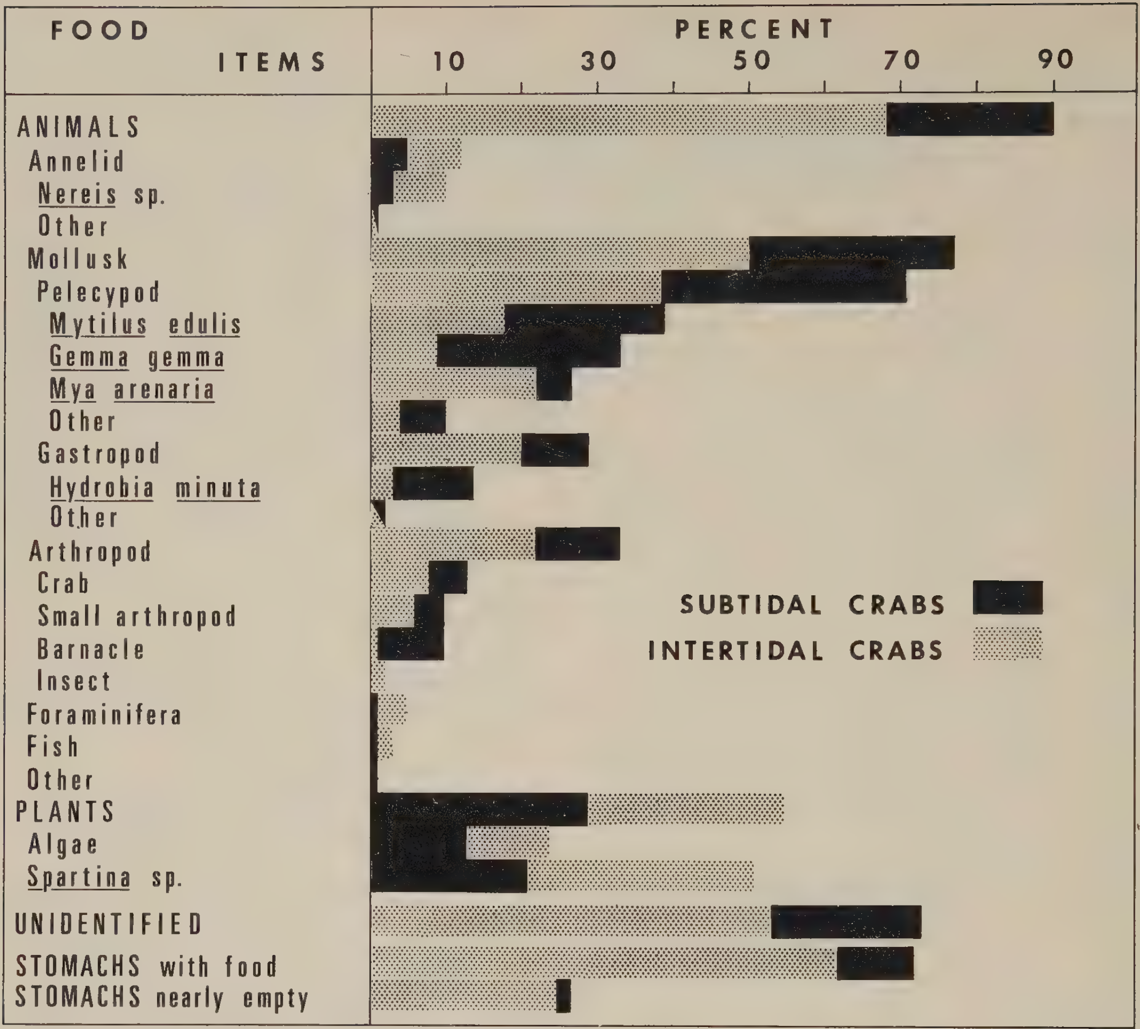
THE INFLUENCE OF CRAB SIZE ON FEEDING HABITS

I analyzed the relation of crab size to stomach contents because food habits sometimes change as an animal grows. The stomach contents differed between crabs less than 30 mm. wide and those 30 mm. wide and larger (fig. 5). The groups are designated as small and large in the text to simplify presentation. The original data on food occurrence are separated by size intervals of 10 mm.

In general, all sizes ingested the same kinds of foods and differences in food were minor. The smallest crabs were perhaps exceptions because fewer different kinds of food were eaten.

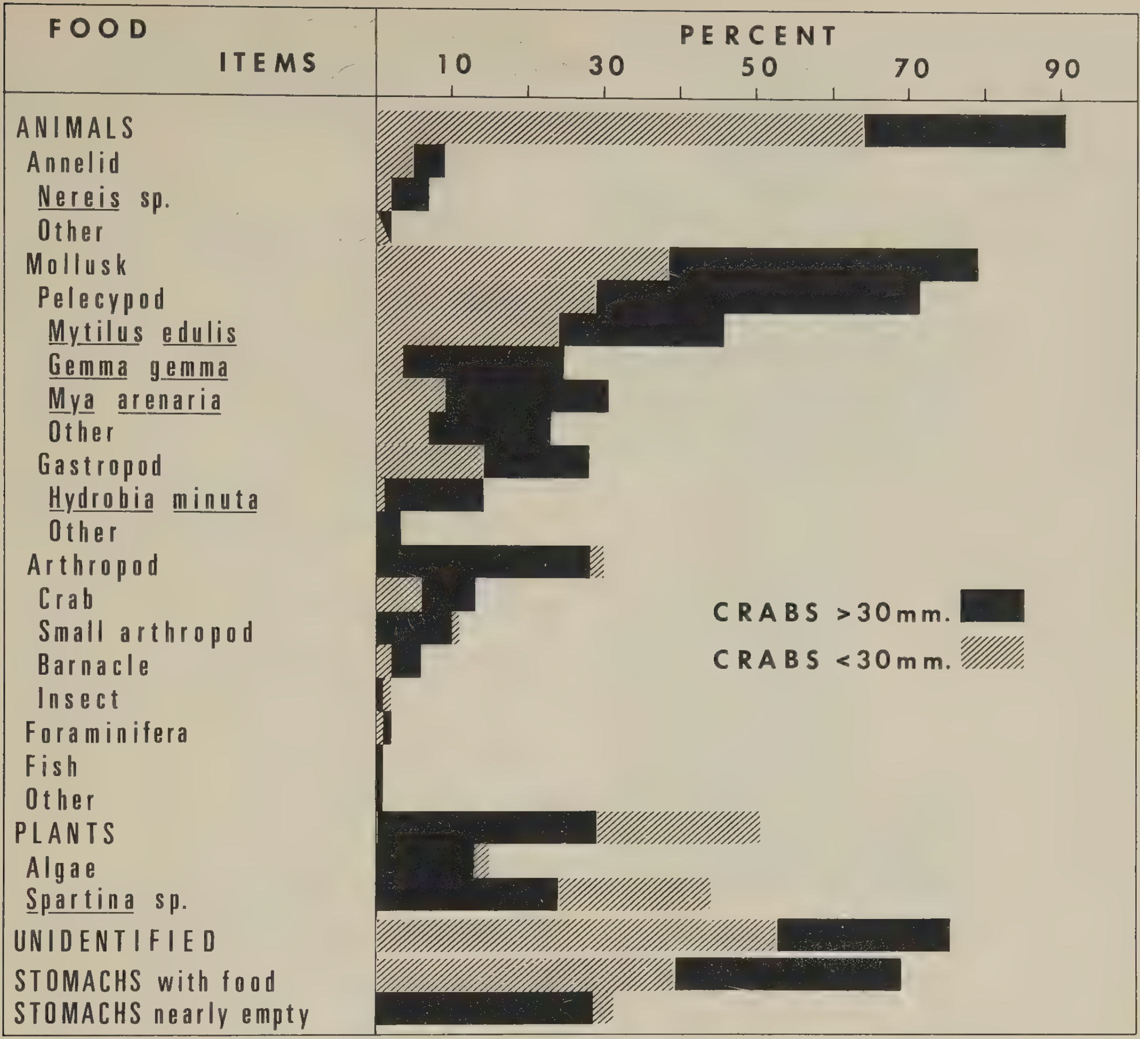
Plants and soft-shelled animals were most frequent in the stomachs of small crabs. More small than large crabs contained *Spartina*, but the frequency of algae was nearly equal in crabs from the two size groups. Small crabs also ate animals, but only small arthropods and insects were more common in small than in large crabs. Numerous stomachs of small crabs contained small, chitinous fragments, probably from small arthropods.

Large crabs contained hard-shelled foods, such as mollusks, more often than did small crabs. Large crabs concentrated on the clam flats when feeding,



FOOD ITEMS	AVERAGE NUMBER	
	INTERTIDAL	SUBTIDAL
Annelid	0.11	0.05
Nereis sp.	.11	.05
Other	<.1	<.01
Mollusk	2.5	17.5
Pelecypod	2.0	10.2
Mytilus edulis	.4	2.3
Gemma gemma	.4	6.7
Mya arenaria	1.0	.9
Other	.1	.2
Gastropod	.6	7.3
Hydrobia minuta	.3	6.7
Other	<.1	<.1
TOTAL NO. of CRABS	847	1,300

FIGURE 4.—The average numbers of certain animals per stomach and the percentage frequency of occurrence of food items in green crabs caught from the intertidal (shaded bars) and subtidal (black bars) zones during 1954 and 1955.



FOOD ITEMS	AVERAGE NUMBER	
	CRABS LESS THAN 30 mm.	CRABS MORE THAN 30 mm.
Annelid	0.03	0.07
Nereis sp.	.02	.06
Other	.01	.01
Mollusk	2.1	15.3
Pelecypod	1.7	10.2
Mytilus edulis	1.0	4.4
Gemma gemma	.1	3.4
Mya arenaria	.2	1.3
Other	.4	1.1
Gastropod	.5	5.0
Hydrobia minuta	.1	4.5
Other	—	.1
TOTAL NO. of CRABS	651	3,328

FIGURE 5.—The average numbers of certain animals per stomach and the percentage frequency of occurrence of food items in small green crabs less than 30 mm. wide (shaded bars) and in large ones 30 mm. wide and larger (black bars).

even though the whole intertidal zone, including the banks where *Spartina* grows, was available to them. Pits dug by green crabs were not found in the banks where some *Mya* lived in the sediments and among the plant roots. Apparently the crabs could not burrow easily into these compact sediments, like the gravel and cobble sediments described by Dow and Wallace (1952). Instead, the green crabs dug numerous pits in the clam flats. Large crabs frequently contained *Mya* and other animals living in the sediments that required some digging to obtain, but few ate *Spartina*.

Most small crabs lived near the banks. Small arthropods, plants, small *Mytilus*, and gastropods, which were frequent in and beneath the vegetation on the banks, provided small crabs with a convenient source of food. Finger-sized holes in the banks, mats of algae, and a thick growth of *Spartina* provided likely protection from predation. Several observations indicated that small crabs inhabited the banks but not the subtidal zone. In 1954, I trapped and dredged green crabs in the subtidal zone and searched the banks for them. All sizes were taken in the banks (fig. 6), but the traps and dredge caught many large, but few small crabs. These observations held true for samples collected during 1955 and 1956. In all 3 years, 47 percent of the 1,323 crabs caught in the intertidal zone and only 1 percent of the 2,656 crabs caught in the subtidal zone were small.

The near absence of small green crabs in the subtidal zone could have been misleading if the mesh size of the dredge (51 mm.) had permitted them to escape. When this same dredge was used on September 6 and 8, 1955, in Rhode Island, however, 108 of the 123 crabs caught were less than 10 mm. wide. These small crabs were picked out of clusters of recently set mussels and also were entangled in algae and eelgrass. Although this example was outstanding, many other dredge samples off Rhode Island included some small crabs and entangling debris. Entangling debris, then, partially closes the dredge meshes and aids in the capture of very small crabs. Debris, in the form of old *Mya* shells and *Spartina*, nearly filled each drag made at Plum Island River, but only one small green crab was caught. Similar debris was occasionally taken at Lufkins Flat, along with 27 small crabs. I conclude that small green crabs were scarce in the subtidal zone at Plum Island River but perhaps were occasionally more abundant at Lufkins Flat than the dredge samples indicated.

THE DIURNAL FEEDING HABITS OF GREEN CRABS

Green crabs are rarely seen in the unflooded intertidal zone during the daytime; most migrate to and from the intertidal zone with the tide (Dexter, 1947; Edwards, 1958), and others hide in bank caves and beneath sods during low water. Both diurnal and tidal activity rhythms were reported for green crabs by Naylor (1958); peaks of activity were during darkness and high tide.

Activity of green crabs in relation to tide and time of day probably affected the results of stomach analyses. The effects of diurnal activities on feeding habits were studied by examining stomachs of crabs dredged during two successive low tides. At most collection dates in 1956, one sample was taken just after sunrise and another late in the afternoon, before sunset. The crabs collected had had the opportunity to feed in the flooded intertidal zone during the high tide preceding capture, during the night or the day, respectively. The total number of stomachs per sample was used to obtain the percentage frequency of occurrence of food items and the average numbers ingested per crab. A preference to feed during a particular time of day is emphasized by this method if either the morning or afternoon samples contain a preponderance of crabs with empty stomachs.

The morning samples had more crabs than the afternoon samples (table 5). A chi-square test indicated significant differences from an expected 1:1 ratio (Plum Island River chi-square=47.42, d.f.=5, $P< 0.01$; Lufkins Flat chi-square=65.72, d.f.=6, $P<0.01$). The number of crabs containing food and the average number of counted food items per crab both were greater in the morning than in the afternoon (fig. 7). Data on crabs with and without food were tested with chi-square (Plum Island River chi-square=6.79, d.f.=1, $P< 0.01$; Lufkins Flat chi-square=29.28, d.f.=1, $P< 0.01$).

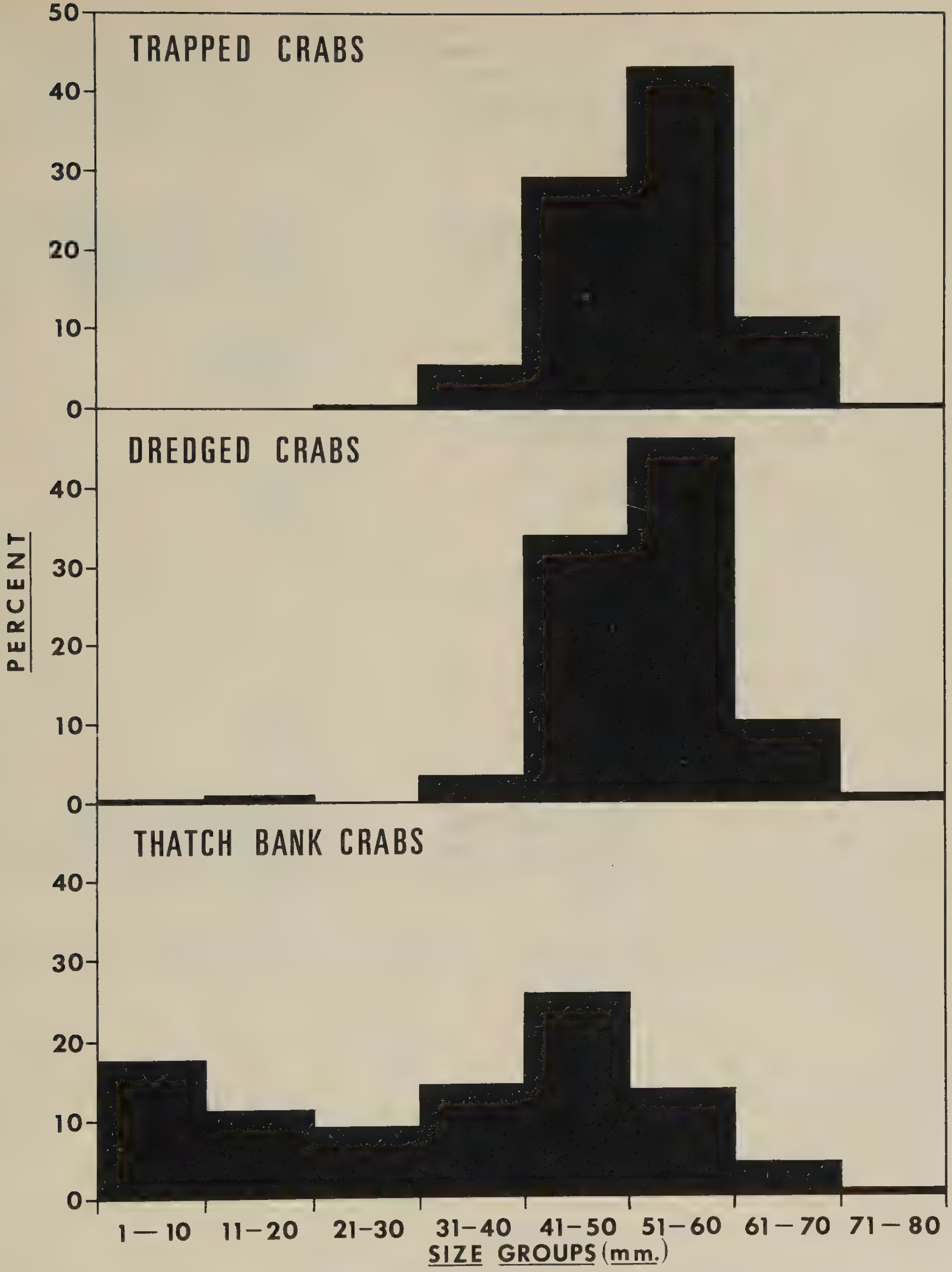
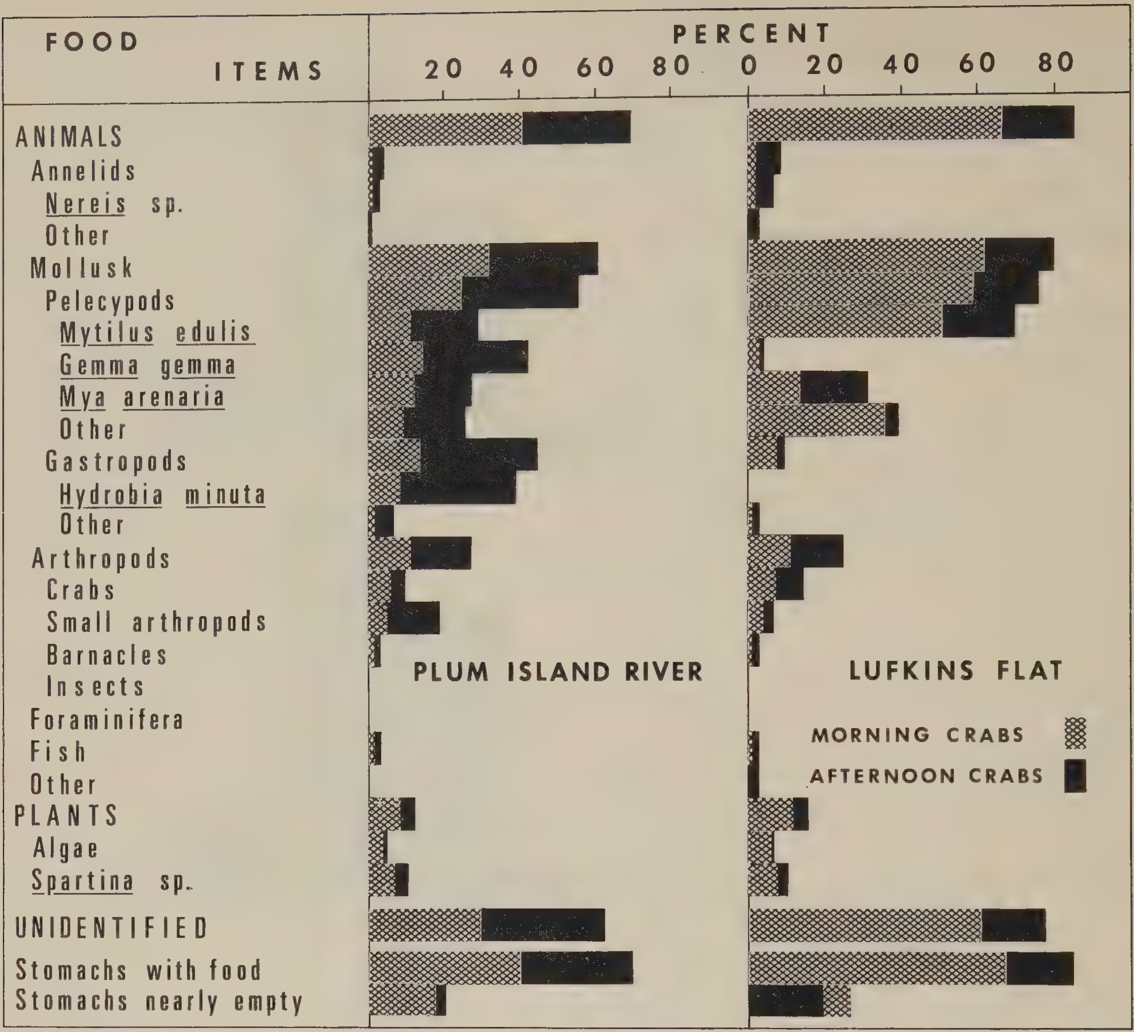


FIGURE 6.—The percentage frequency of occurrence, by 10-mm. size groups, of green crabs dug from the thatch banks in the intertidal zone and dredged and trapped in the subtidal zone during 1954.



FOOD ITEMS	AVERAGE NUMBER			
	MORNING	AFTERNOON	MORNING	AFTERNOON
Annelids	0.03	0.0	0.03	0.02
Nereis sp.	.02	.0	.03	.02
Other	.01	.0	.0	.0
Mollusks	17.3	3.8	13.1	12.1
Pelecypods	6.0	1.9	12.6	12.0
Mytilus edulis	1.0	.5	9.2	8.1
Gemma gemma	3.1	.7	<.1	<.1
Mya arenaria	.9	.4	1.4	.7
Other	1.0	.4	2.0	3.1
Gastropods	11.3	1.8	.5	.1
Hydrobia minuta	10.8	1.4	.0	.0
Other	.2	.1	.3	<.1
TOTAL NO. of CRABS	271	169	403	296

FIGURE 7.—The average numbers of certain animals per stomach and the percentage frequency of occurrence of food items in green crabs dredged in the morning (shaded bars) and afternoon (black bars) during 1956 at Plum Island River and Lufkins Flat.

TABLE 5.—*Number of green crabs caught in the morning and afternoon at Plum Island River and Lufkins Flat during 1956*

Locality and date	Drags during each morning and each afternoon	Crabs caught during collection period		Total crabs
		Morning	Afternoon	
Plum Island River	*Number*	*Number*	*Number*	*Number*
June 11	6	34	22	56
July 23	8	27	26	53
Aug. 6	9	25	25	50
Sept. 4	6	67	10	77
Sept. 21	2	26	26	52
Oct. 19	4	61	9	70
Total	35	240	118	358
Lufkins Flat				
June 11	5	26	16	42
July 23	5	59	20	79
Aug. 6	5	52	20	72
Sept. 5	8	54	53	107
Sept. 22	8	45	46	91
Oct. 5	4	49	4	53
Oct. 20	3	98	12	110
Total	38	383	171	554

OTHER FACTORS THAT INFLUENCE FEEDING HABITS

TEMPERATURE

The food consumption of the green crab may be affected by extremes in water temperature. Green crabs were presumed to be influenced by adverse temperature if less than half of the stomachs had food; if more than half of the stomachs with food were also nearly empty; and if no other factors were suspected to have prevented feeding.

The number of crabs containing food clearly declined in eight samples from the intertidal zone (table 6); seven samples were collected when the water temperatures were 11.5° C. and lower, and the crab stomachs contained only shell fragments; and one sample was collected when the water temperature was 26° C. Two other samples were borderline examples because slightly more than half of the crabs had recently fed. If the sample on August 26, 1955 is excluded, the total of 9 samples included 696 crabs; 208 contained food, but of these 129 (62 percent) were nearly empty. Thus, only 79 (38 percent) had eaten when the temperatures were 12° C. or less.

Eleven intertidal samples contained crabs that had clearly been feeding when the water temperatures were 9° C. or higher (table 6). The total of 11 samples included 619 crabs; 431 contained food, and only 82 (19 percent) of these were nearly empty. Therefore, 349 of the crabs (81 percent) had eaten when the temperatures were 9° C. or higher.

TABLE 6.—*Water temperatures and the percentage frequency of occurrence of food in green crabs from the intertidal zone, 1954–55*

Date	Temperature	Crabs with food	Crabs recently fed	Crabs with nearly empty stomachs	Total crabs
1954	° *C.*	*Percent*	*Percent*	*Percent*	*Number*
Sept. 16	(1)	60	90	10	35
Sept. 23	16.0	61	68	32	51
Oct. 5	16.5	68	56	44	50
Oct. 19	(1)	76	86	14	72
Oct. 22	13.0	82	100	0	11
Nov. 2	9.6	83	94	6	93
Nov. 5	9.0	79	79	21	96
Nov. 18	(1)	62	89	11	113
Dec. 6	.0	11	38	62	72
Dec. 8	2.5	44	30	70	45
Dec. 22	1.0	27	38	62	155
1955					
Jan. 12	0	0	0	0	27
Jan. 27	.7	23	10	90	44
Feb. 16	2.0	29	17	83	83
Apr. 18	11.5	39	25	75	83
May 19	15.0	64	74	26	36
July 23	18.0	55	85	15	49
Aug. 26	26.0	38	33	67	8
Oct. 21	12.0	62	37	63	13
Oct. 21	10.5	42	58	42	137
Nov. 23	2.0	30	53	47	50

(1) No observation.

Most crabs caught in the subtidal zone were collected when the water was warm. A few exceptions indicated feeding at temperatures lower than 12° C. Table 7 includes the dates when the water temperatures at the dredge sites were less than 12° C. More than 50 percent of the crabs sampled on or near these dates contained food and less than half of the stomachs containing food were classified as nearly empty. These data suggested that temperatures as low as 7° C. do not suppress feeding. Activity, and presumably feeding as well, probably ceased at some temperature below 7° C. because on November 23, 1955, when the water temperature was 2° C., no green crabs were caught in the subtidal zone at either sampling area.

TABLE 7.—*Low water temperatures and the percentage frequency of occurrence of food in green crabs from the subtidal zone at Plum Island River and Lufkins Flat, 1954–56*

Place and date	Temperature	Crabs with food	Crabs recently fed	Crabs with nearly empty stomachs	Total crabs
Plum Island River	° *C.*	*Percent*	*Percent*	*Percent*	*Number*
Nov. 5, 1954	9.0	68	69	31	62
Nov. 7, 1955	10.0	90	61	39	49
May 11, 1956	10.0	50	0	0	2
Oct. 5, 1956	10.0	79	77	23	62
Oct. 19, 1956	10.0	87	83	17	61
Nov. 15, 1956	7.5	67	87	13	24
Lufkins Flat					
Apr. 18, 1955	11.5	55	36	64	20
Oct. 21, 1955	10.5	77	65	35	44
Nov. 7, 1955	10.0	83	84	16	69
May 11, 1956	8.0	85	80	20	58
Oct. 20, 1956	9.5	95	83	17	98
Nov. 5, 1956	7.0	93	88	12	71

SALINITY

The feeding of green crabs was limited less by low salinities than by low temperatures in Plum Island Sound. Green crabs maintain a homoiosmotic condition when subjected to diluted sea water by actively taking up ions through the gills, increasing their oxygen consumption, and expending energy (Scheer, 1948; Waterman, 1960). Duval (1925) found that green crabs lived permanently in salinities as low as 11 p.p.t. (parts per thousand), but lower salinities killed them within 24 to 48 hours. Green crabs sometimes seek temporary shelter in moist caves, crevices, and seaweeds when the water in the estuary is drastically diluted (Broekhuysen, 1936; Nicol, 1935).

Salinities fell below 11 p.p.t. only at Plum Island River and only on three occasions (table 8). The proportions of crabs containing food were similar during periods of high and low salinity. Only slightly fewer crabs were caught per drag and fewer food items were counted in the stomachs of crabs caught when the salinity was low. The influence of low salinity on feeding was not apparent, even though the values were below the reported tolerance limits for green crabs.

TABLE 8.—*Low salinity and the percentage frequency of occurrence of food in green crabs at Plum Island River, 1955–56*

Date	Salinity	Crabs with food	Crabs recently fed	Crabs with nearly empty stomachs	Total crabs
	p.p.t.	*Percent*	*Percent*	*Percent*	*Number*
Apr. 18, 1955	9.0	75	87	13	20
Nov. 7, 1955	7.4	90	61	39	49
May 11, 1956	7.6	50	0	0	2

SEX

Female green crabs were sometimes predominant in the dredge catches. An analysis of the sex ratio and frequency of occurrence of food by sex indicated that feeding differed with sex at Plum Island River.

Many more female than male crabs from Plum Island River contained mollusks (fig. 8). Six other food items also occurred slightly more often in female than male crabs. Female crabs from Plum Island River were only slightly more numerous than males in the total catch and were relatively more abundant than males for a shorter period of time than at Lufkins Flat (fig. 9). The total predation on mollusks by female crabs at Plum Island River was greater than by males, not only because more females were present to feed at certain times of the year, but because they ate more mollusks than did the males.

Differences were not appreciable between the stomach contents of male and female crabs caught from Lufkins Flat (fig. 8), but more female than male crabs were caught in nearly every collection (fig. 9). The total predation by females was greater than that by males only because females were more abundant.

EGG BEARING

In both sample areas fewer ovigerous crabs contained food (table 9) than nonovigerous, even though the kinds of food eaten by the two types of crabs were the same. The reduction in food intake may be accounted for by Dearborn's[4] observations that although ovigerous crabs readily accepted food in the laboratory, they are generally less active. The dredge catches indicated that fewer ovigerous than nonovigerous crabs were feeding; only 5.5 percent of the females from Plum Island River and 4.6 percent from Lufkins Flat were ovigerous.

TABLE 9.—*Percentage frequency of occurrence of ovigerous and nonovigerous female green crabs that contained food at Plum Island River and Lufkins Flat, 1955–56*

Female condition and place	Crabs with food	Crabs recently fed	Crabs with nearly empty stomachs	Total females
	Percent	*Percent*	*Percent*	*Number*
Ovigerous				
Plum Island River	29	56	44	31
Lufkins Flat	51	42	58	47
Nonovigerous				
Plum Island River	67	70	30	529
Lufkins Flat	80	72	28	981

MOLTING

As with other crustaceans, the green crab must molt its hard exoskeleton to grow. While preparing for ecdysis and hardening the exoskeleton after ecdysis, the crab would be likely to change its feeding habits because its claws and mouthparts are too soft to handle some of the usual foods. To determine the degree of change in food during molting, green crabs caught during 1956 were separated into five groups, based on molting condition. One group, the premolt crabs, was

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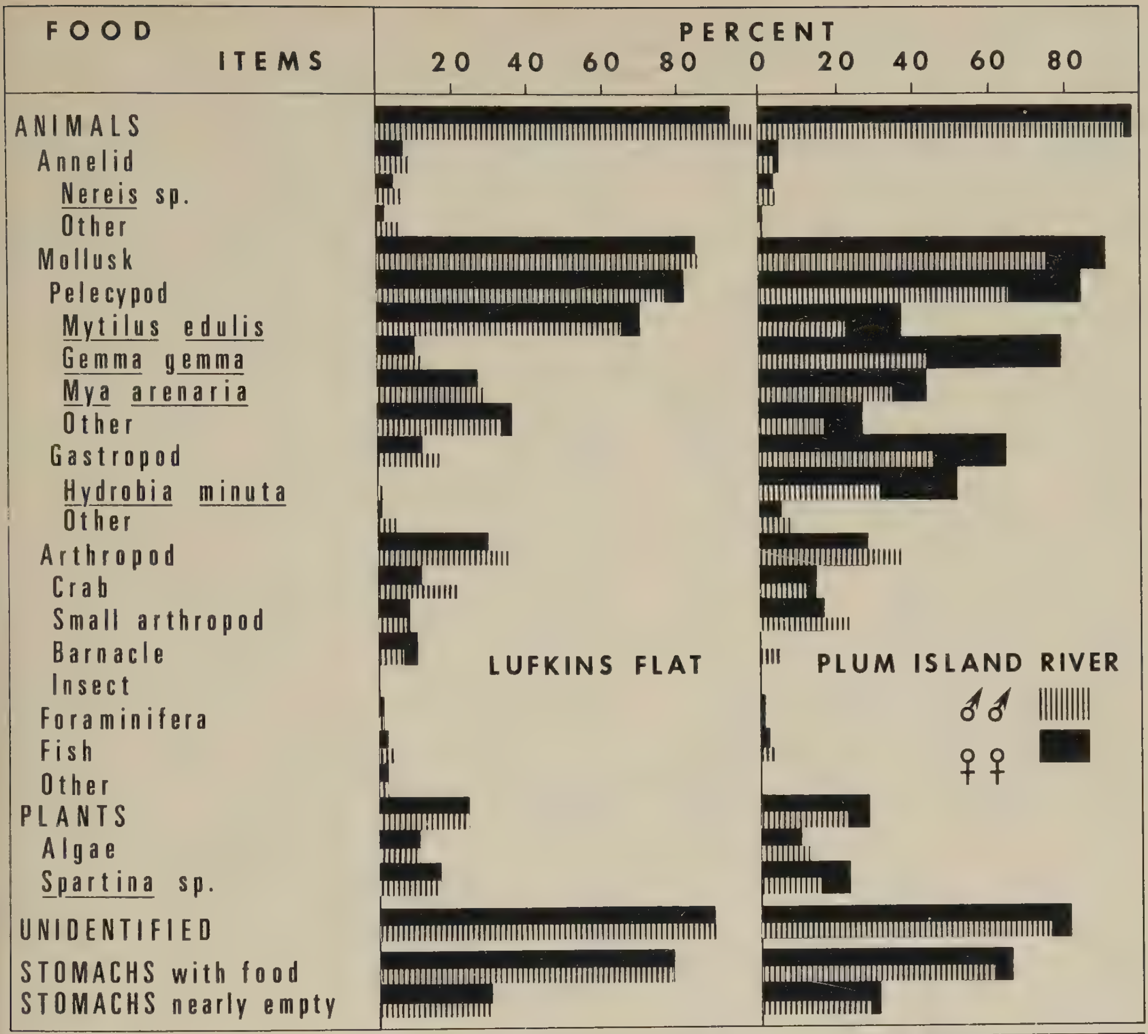
[4] Footnote 1.



FOOD ITEMS	AVERAGE NUMBER			
	MALES	FEMALES	MALES	FEMALES
Mollusk	13.2	13.1	23.3	6.1
Pelecypod	12.0	12.7	10.1	15.4
Mytilus edulis	8.1	8.5	.5	1.8
Gemma gemma	1.4	.7	8.4	11.0
Mya arenaria	1.1	1.5	.8	1.6
Other	1.4	2.1	.4	1.0
Gastropod	.7	.5	13.2	17.8
Hydrobia minuta	.3	.1	12.3	17.2
Other	.1	.2	.2	.2
TOTAL NO. of CRABS	350	1,028	505	560

FIGURE 8.—The average numbers of certain animals per stomach and the percentage frequency of occurrence of food items between the sexes of green crabs caught during 1955 and 1956 (males, shaded bars; females, black bars)

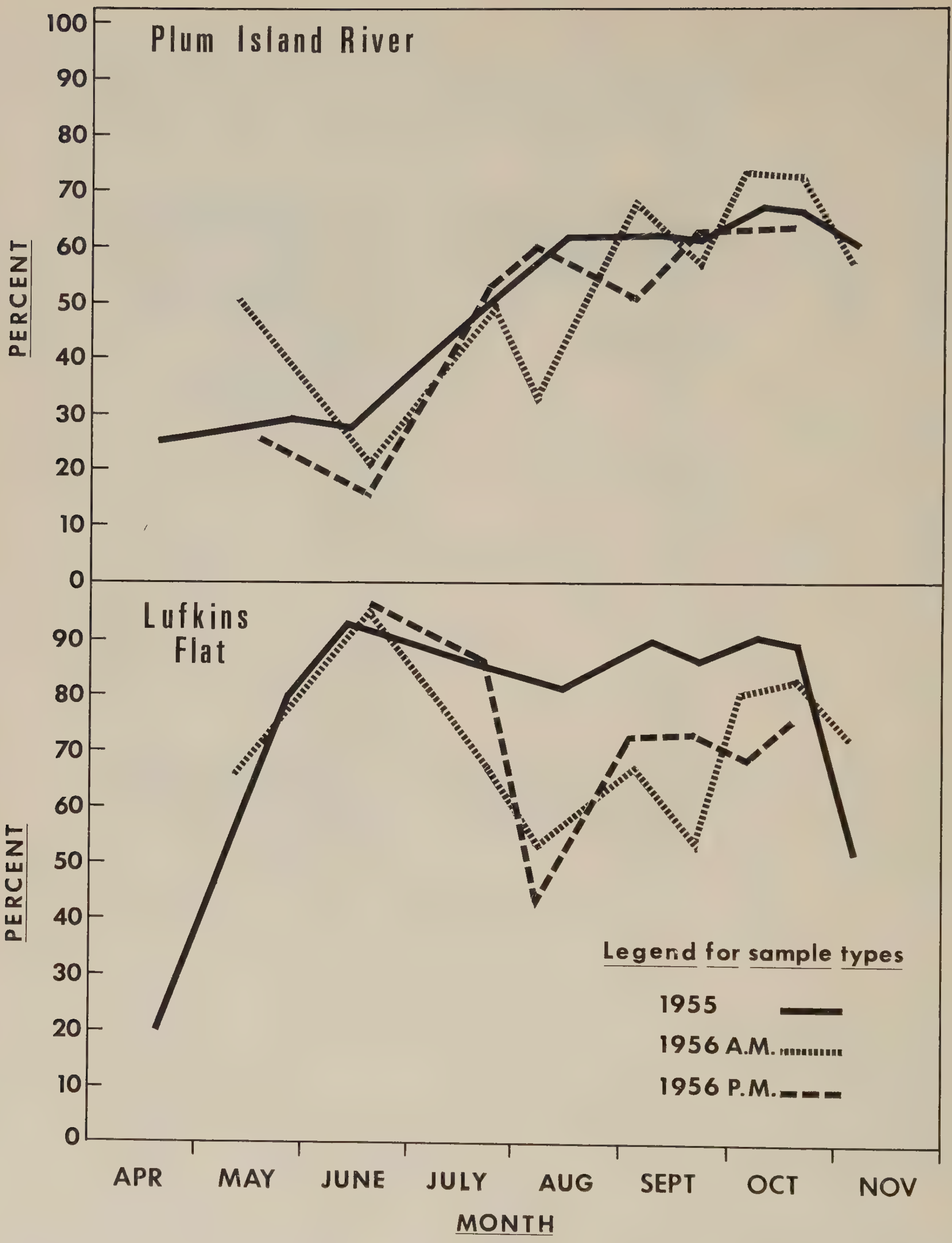


FIGURE 9.—The percentage frequency of occurrence of female green crabs in the dredge catches at Plum Island River and Lufkins Flat during 1955 and 1956.

easily separated while the stomachs were examined because the old stomach is replaced just before ecdysis. A second group included recently molted crabs with very soft shells. The next two groups, moderately soft-shelled and nearly hard-shelled crabs, were separated on the basis of the ease with which the carapace indented under finger pressure. The carapaces of hard-shelled crabs, the fifth group, were rigid and cracked if enough force was exerted.

The food habits of premolt and recently molted crabs were particularly affected (fig. 10). A few of these crabs contained bits of shell presumably ingested before ecdysis took place. Thus, like other brachyuran crabs (Waterman, 1960), green crabs stop feeding just before and after ecdysis.

Occurrence of food increased as the shells of molted crabs progressively hardened. Most of the moderately soft-shelled and nearly hard-shelled crabs contained *Gemma*, *Hydrobia*, small arthropods, and algae, and all of the typical foods were found in both groups. All foods, except those mentioned for moderately soft-shelled crabs, occurred more often and in larger numbers in nearly hard-shelled crabs than in any other group. This finding suggested that nearly hard-shelled crabs had a greater appetite than hard-shelled crabs. Nevertheless, the total predation by hard-shelled crabs was greater than that of nearly hard-shelled crabs because the crabs are in the hard-shelled condition for a longer period of time (Waterman, 1960).

MATING

Stomach analysis of a few male crabs, each caught clasping a female, indicated that they ceased feeding during the mating act. Only 2 of the 10 mated males from Plum Island River contained food, and both were nearly empty. No mated pairs were caught at Lufkins Flat.

THE GENERAL PREDATORY ECOLOGY OF GREEN CRABS

Green crabs eat other foods than those listed in table 1. I collected stomachs from Maine which contained *Anomia* sp., whereas *Aquipecten irradians* and *Zostera marina* occurred in some from Rhode Island. Spear [5] found during a laboratory study that green crabs ate small hard clams, *Mercenaria mercenaria* (6–10 mm.), in preference to larger ones (20–25 mm.). Green crabs almost destroyed small hard clams planted experimentally in Wickford Harbor, R.I., by Warren S. Landers (oral communication). Dearborn [6] found the following foods acceptable to green crabs: *Crassostrea virginica*, *Astarte castanea*, *Pectin grandis* (=*Placopecten magellanicus*), *Nucula* sp., *Modiolus modiolus*, *Callocardia* (=*Pitar*) *morrhuana*, *Spisula solidissima*, *Saxicava* (=*Hiatella*) *arctica*, *Fundulus* sp., *Laminaria* sp., *Littorina littorea*, and *L. obtusata*. Such variety in the diet of green crabs is undoubtedly due to their omnivorous feeding habits.

The green crab's ability to grasp, crush, and tear apart food probably permits scavenging for foods such as dead fish; however, they are not exclusively scavengers because they eat many live foods and may actually prefer fresh food to carrion. Fishermen replace old decomposed bait because they say fresh bait catches more green crabs. Some fresh, recently killed food is available from natural causes. While using free diving gear, I saw green crabs quickly pick up and eat small herring that sank to the bottom after being killed or stunned by gulls.

Samples of crabs taken by traps or dredges or from bank caves indicated that the population of green crabs in Plum Island Sound was large. Evidence of intraspecific competition was meager, however, even though the foods eaten by all sizes of crabs were qualitatively similar. The incidence of cannibalism, a possible measure of extreme competition, was low. Actually there was more reason to suppose that intraspecific competition was circumvented. Small crabs, which would be the most vulnerable to cannibalism because of their size, did not mix with the large crabs. Presumably the separation of small from large crabs enabled them to grow and develop their food-gathering abilities without the necessity of competing with large crabs. The omnivorous feeding of green crabs also serves to reduce intraspecific competition and to permit a large population to inhabit an area.

Predator control methods, developed during investigations of the decline in soft-shell clams, reduced the effects of green crabs on the clam flats. Fences (Smith, 1954; Smith et al., 1955) and

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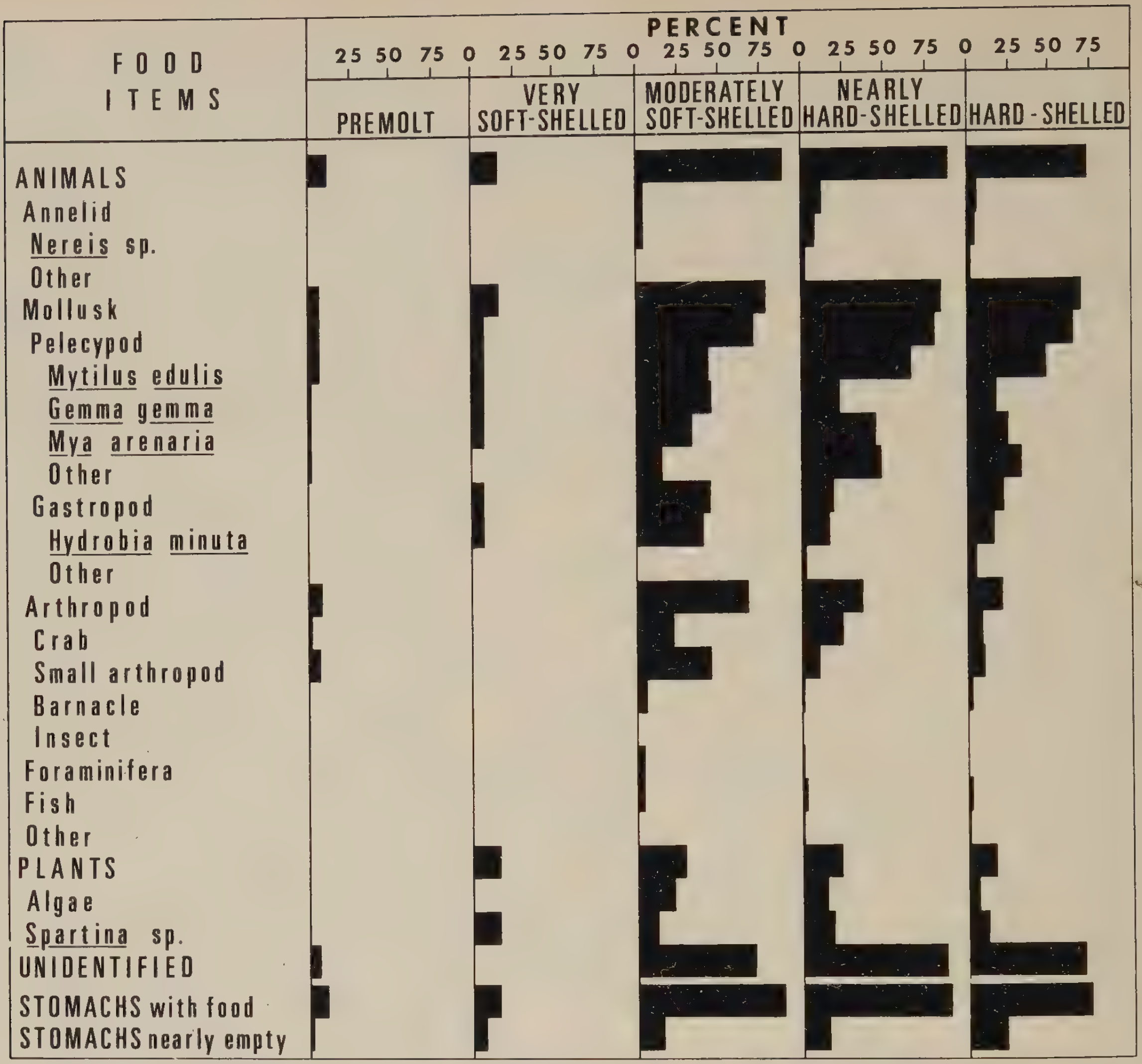
[5] Spear, Harlan S. 1955. Notes on laboratory experiments on feeding habits of green crabs. [U.S.] Fish Wildl. Serv., Clam Invest., Boothbay Harbor, Maine, 5th Conf. Clam Res.: 45. [Mimeographed.]

[6] Footnote 1.



FOOD ITEMS	AVERAGE NUMBER				
Annelid	0.0	0.0	0.0	0.07	0.02
Nereis sp.	.0	.0	.0	.07	.01
Other	.0	.0	.0	.0	<.01
Mollusk	.1	.3	10.0	28.9	10.8
Pelecypod	.1	.3	7.0	22.6	7.9
Mytilus edulis	.1	.0	1.5	14.8	4.6
Gemma gemma	<.1	.2	3.4	1.4	.9
Mya arenaria	.1	.1	.6	3.2	.9
Other	<.1	.0	1.4	3.2	1.6
Gastropod	.0	.1	3.0	6.3	3.0
Hydrobia minuta	.0	.1	2.9	6.0	2.6
Other	.0	.0	.0	.1	.2
TOTAL NO. of CRABS	43	15	37	217	1,044

FIGURE 10.—The average numbers of certain animals per stomach and the percentage frequency of occurrence of food items in green crabs before and after molting.

chemical barriers (Hanks, 1961) were used to control predation by green crabs. These devices were usually installed in an area during early spring and maintained until late fall because green crabs feed for 6 to 7 months of the year.

The entire population of crabs may not be feeding actively at any one time in Plum Island Sound. Few ovigerous females were caught by dredging, but many of these samples were taken when, according to Broekhuysen (1936), ovigerous females would be scarce. Nevertheless, this study and unpublished records of green crabs caught by the staff of the Bureau of Commercial Fisheries indicated that ovigerous females were generally less active than nonovigerous crabs. A total of 124 females and 4 males were caught in three collections from the outflow of a hydraulic dredge that was excavating channels in the Merrimack River basin during June 1953; 94 percent of the females were ovigerous. At the same time traps and a scallop dredge fished near the area caught 24 males and 31 females, but only one of the females was ovigerous. Apparently ovigerous females are generally inactive and buried in the bottom substrate where the scallop dredge does not catch them.

The inconsistent feeding habits of each sex in the two areas sampled suggested that some aspect of their behavior may also be dissimilar. Male green crabs actively seek females that are about to molt, as they can mate only with soft-shelled individuals. It is not completely known how males select females that are about to molt, but Broekhuysen (1936) believed that as female crabs approach ecdysis they become passive to the advances of male crabs. Upon finding such a female, the male picks her up and holds her upside down beneath his body. The female may be carried by the male for several days before the female molts and mating takes place. While seeking and holding a female, the male's search for food probably is restricted.

To obtain indirect evidence of readiness for mating, I counted female green crabs in the premolt condition (data combined for 1955 and 1956) and found 4.8 percent at Plum Island River and 0.5 percent at Lufkins Flat. Males in the Plum Island River area, then, may have been more actively seeking mates than feeding because molting females were more available there. The time spent seeking and holding a mate may have contributed to the observed differences in the feeding habits between the sexes at Plum Island River.

These observations do not contradict Dearborn's[7] conclusion that male and female green crabs have similar food habits, because he held each crab in a separate container. In the absence of mates, male crabs probably had feeding habits similar to those of nonmolting females, and were, thus, like the crabs caught at Lufkins Flat.

Female green crabs were probably more destructive than males to the soft-shell clam population in Plum Island Sound. At least, relatively more female crabs were caught at both sample areas during the fall, when Smith (1955) found newly settled juvenile *Mya* abundant. An abundance of small-sized food, at a period in the crab's life history when molting, mating, low temperatures, and salinity were minor factors limiting the population's feeding habits, undoubtedly contributed to the decline of the clam fishery in Plum Island Sound.

SUMMARY

1. The green crab is an omnivore, but pelecypods formed a dominant part of the diet of crabs collected from Plum Island Sound, Mass., and vicinity.

2. Green crabs exhibit raptorial feeding abilities, aided by accessory organs which direct them to sources of food. The abundance, size, and kind of foods influence feeding.

3. Pelecypods were most frequent in crabs 30 to 59 mm. wide even though all sizes contained essentially the same kinds of food.

4. The feeding habits of green crabs were regulated by the time of day and the tides. The greater frequency of food in crabs caught during low tide and just after sunrise suggests that feeding is heaviest at night and at high tide.

5. Activity, and presumably feeding as well, probably were restricted at water temperatures below 7° C.

6. Low salinity apparently did not influence feeding.

7. Female crabs were relatively more numerous than males in the fall and, thus, were probably more destructive of pelecypods in Plum Island Sound.

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[7] Footnote 1.

8. Ovigerous females were relatively inactive and, thus, less destructive of pelecypods than nonovigerous females.

9. Feeding by crabs preparing for ecdysis and subsequent hardening of the exoskeleton was generally reduced, except for crabs that had nearly hard shells.

10. Feeding of male crabs apparently is markedly reduced during the mating act.

ACKNOWLEDGMENTS

Fenner A. Chace, Jr., Curator, Division of Marine Invertebrates, U.S. National Museum, provided the taxonomic background for the valid generic name of the green crab, namely, *Carcinus* rather than *Carcinides*. Lionel Sheppard, former Clam Commissioner of Ipswich, Mass., assisted during many of the dredge collections. Franklin C. Daiber of the University of Delaware read the manuscript and made helpful suggestions.

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EARLY LIFE HISTORY AND SPAWNING OF THE ALBACORE, *THUNNUS ALALUNGA*, IN HAWAIIAN WATERS

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ABSTRACT

Thirty-five juvenile albacore were found in the stomachs of 4,568 billfishes captured in Hawaiian waters between July 1962 and April 1966.

Regressions of standard length on lengths of various segments of the vertebral column, determined from measurements made on 21 intact specimens caught in the Pacific Ocean, were used to estimate the lengths of the fragmentary specimens. A linear regression was used to describe the first year's growth of albacore. By use of the regression, expected lengths for various ages, in days, up to 1 year were obtained. One-year-old albacore were estimated to be 38 cm. in standard length. The spawning season for albacore in Hawaiian waters peaks in May and probably extends from March to September.

The albacore (*Thunnus alalunga*) in the North Pacific are believed to constitute a single subpopulation, the adults of which support fisheries off the coasts of North America and Japan. The age and growth of adult albacore have been estimated and hypotheses have been developed on their migrations among the fisheries (Otsu, 1960; Clemens, 1961; Otsu and Uchida, 1963).

Basic information on young albacore before they are recruited into the commercial fisheries is sketchy, however. Descriptions of larval albacore appear in the literature, but they need verification. Matsumoto's (1962) description of larval albacore differs significantly from that of Yabe and Ueyanagi (1962). Yabe, Ueyanagi, Kikawa, and Watanabe (1958) and Yoshida (1965) published descriptions of the anatomy of juvenile albacore, and Asano (1964) published observations on the morphology. The present report treats aspects of the early life history of albacore before their recruitment into the commercial fisheries. Growth in the first year of life is estimated and inferences are made on the spawning habits of the adults.

The juvenile albacore for this study came from the stomachs of billfishes, which are good collectors of juvenile tunas (Yabe et al., 1958; Yoshida, 1965). The Honolulu fish markets were an excellent source of billfishes from which stomachs could be sampled with relatively little difficulty. Although the abundance of billfishes varied seasonally, stomachs were available from every month in a 46-month period between 1962 and 1966. The billfish stomachs yielded 35 juvenile albacore. Skipjack tuna (*Katsuwonus pelamis*), the most numerous juvenile tuna, was about 24 times more numerous than albacore. Smaller numbers of juvenile yellowfin tuna (*T. albacares*), bigeye tuna (*T. obesus*), and other tunas and tunalike fishes were found.

COLLECTION AND EXAMINATION OF STOMACHS

Stomachs of 4,568 billfishes were examined from July 1962 to April 1966—3,751 striped marlin (*Tetrapturus audax*), 477 blue marlin (*Makaira nigricans*), 268 shortbill spearfish (*Tetrapturus angustirostris*), 34 black marlin (*Makaira indica*), 31 sailfish (*Istiophorus orientalis*), and 7 unidentified billfishes. The stomachs of striped marlin, blue marlin, and shortbill spearfish contained juvenile albacore.

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Most of the stomachs came from billfishes captured by vessels of the Hawaiian longline fishery. Otsu (1954) and Shomura (1959) gave detailed descriptions of that fishery. The catches are landed at the United Fishing Agency and the Fishing Co-Op of Hawaii in Honolulu, where the fish are sold at auction. The stomachs and information on the date of landing, locality of capture, weight, and sex for each fish were made available by the fish market personnel or the purchasers of the fish.

The vessels usually fished within sight of land. Thus, most of the stomachs came from billfishes captured within about 37 km. of the main Hawaiian islands. A few of the stomachs, however, came from billfishes caught as far as 644 km. from Oahu.

From 1962 to 1965, stomach samples were also collected from billfishes captured in the Hawaiian International Billfish Tournament, held annually since 1959 at Kona, Hawaii. The rules of the tournament limited the fishing area to the lee of the island of Hawaii.

The striped marlin were 4 to 148 kg.; the size distribution showed modes between 16 and 20 kg. and between 36 and 40 kg. The blue marlin were 16 to 364 kg.; a prominent mode was present between 60 and 70 kg. The shortbill spearfish were 14 to 38 kg.; a mode was present between 12 and 16 kg. The sailfish were 14 to 38 kg.; black marlin, from 36 to 290 kg.

The stomach samples from the Honolulu markets were taken to the laboratory and either examined immediately or preserved in 10 percent Formalin[1] for later examination. The samples from the billfish tournaments were shipped to the laboratory after preservation in 10 percent Formalin. In the laboratory, the stomach contents were initially sorted for tuna and tunalike specimens, which were later identified to species. The tuna specimens, which were affected in varying degrees by digestion, could be identified by their skeletons (Yabe et al., 1958; Matsumoto, 1963; Yoshida, 1965).

LENGTH OF JUVENILE ALBACORE

Few juvenile albacore from the billfish stomachs were intact. To estimate the SL (standard length) of the fragmentary specimens, which usually included part of the vertebrae, I determined the relation between the standard length and the lengths of various vertebral segments. On 21[2] relatively undamaged specimens (table 1) I measured the standard length, lengths of the vertebral column (39 vertebrae), precaudal vertebrae (1st–18th vertebrae), caudal vertebrae (19th–39th vertebrae), 1st to 9th vertebrae, and 19th to 28th vertebrae. The data indicated that all the relations were linear. The regressions describing the relations are:

Standard length on length of:

(1) vertebral column, $l = -0.2825 + 1.2762L$ $(s=0.218)$,

(2) precaudal vertebrae, $l = 0.0634 + 2.8843L$ $(s=0.429)$,

(3) caudal vertebrae, $l = -0.4370 + 2.2744L$ $(s=0.298)$,

(4) 1st–9th vertebrae, $l = 0.3200 + 6.3963L$ $(s=0.788)$,

(5) 19th–28th vertebrae, $l = -0.4579 + 4.4282L$ $(s=0.289)$,

where l is the standard length (cm.), L is the length (cm.) of the vertebral fragments, and s is the standard deviation from regression.

TABLE 1.—*Measurements of standard length and various vertebral column lengths of 21 juvenile albacore found in stomachs of billfish caught in Pacific Ocean*

Specimen No.	Standard length	Length vertebral column	Length precaudal vertebrae	Length caudal vertebrae	Length 1st–9th vertebrae	Length 19th–28th vertebrae
	Mm.	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*
1	85	68	30	38	13	20
2	88	69	29	39	13	20
3	74	61	25	35	10	18
4	257	200	86	114	38	58
5	354	281	122	159	54	81
6	105	85	35	50	17	25
7	184	147	65	83	29	43
8	143	116	50	66	19	34
9	78	62	25	37	11	18
10	119	97	43	54	19	28
11	118	94	41	53	18	28
12	113	90	38	52	19	27
13	113	92	40	52	18	27
14	121	99	42	57	19	29
15	99	80	34	46	15	24
16	53	41	17	23	8	12
17	86	71	31	40	14	20
18	328	257	112	145	53	75
19	230	182	80	102	35	53
20	230	184	83	101	35	52
21	185	149	64	85	27	44

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[1] Trade names referred to in this publication do not imply endorsement of commercial products.

[2] These specimens were from stomachs of predators captured not only in Hawaiian waters but in various localities in the North and South Pacific. I believe this fact should not affect the results. A covariance analysis applied to the relation between standard length and vertebral column length for North and South Pacific juvenile skipjack tuna showed no significant differences between the samples in the mean vertebral column length and slope of the lines.

I estimated the lengths of 26 of the 35 specimens with the regressions. The longest vertebral fragment available was always used to estimate the lengths. For example, if the vertebral column was intact, the regression with the length of all vertebrae as the variable was used rather than any of the other regressions. Pertinent data on the juvenile albacore are in table 2.

Table 2.—*Record of juvenile albacore from stomachs of billfishes caught in Pacific Ocean, 1962–66*

Date	Albacore	Predator		
	Standard length	Species	Weight	Location of capture (off the coast of)
	Cm.		*Kg.*	
August 1, 1962 [1]	18.4	Blue marlin	132.4	Kona, Hawaii.
August 13, 1962 [1]	[2] 13.0	Striped marlin	29.5	Waianae, Oahu.
September 13, 1962.[1]	[2] 18.1	Blue marlin	93.9	Do.
November 2, 1962 [1]	25.7	Striped marlin	29.9	Do.
Do	[2] 28.0	do	32.2	Do.
August 16, 1963	[2] 11.1	do	19.5	Do.
September 16, 1963	[2] 14.2	Blue marlin	65.8	Kalapana, Hawaii.
November 4, 1963	[2] 16.0	Shortbill spearfish.	15.9	Do.
November 7, 1963	[2] 11.9 [2] 11.4	Blue marlin	59.4	Do.
February 6, 1964	[2] 31.0	Striped marlin	19.5	Napoopoo, Hawaii.
February 20, 1964	35.4	do	147.9	241 km. south of Oahu.
February 25, 1964	[2] 33.6 [2] 35.5	do	17.2	161 km. south of Oahu.
March 4, 1964	[2] 34.6	do	26.8	West Lanai.
March 17, 1964	[2] 35.0	do	20.9	Waianae, Oahu.
June 29, 1964	[2] 9.5	Shortbill spearfish.	10.9	Do.
July 17, 1964	[2] 11.0	do	12.7	483 km. south of Oahu.
July 27, 1964	[2] 9.0	Striped marlin	12.7	Waianae, Oahu.
August 3, 1964	[2] 12.8	Shortbill spearfish.	10.9	483 km. south of Oahu.
September 15, 1964	[2] 9.5	do	13.6	Upolu Pt., Hawaii.
November 3, 1964	[2] 14.5	Striped marlin	39.9	Waianae, Oahu.
August 24, 1965	[2] 12.0	Blue marlin	52.2	Do.
Do	[2] 7.8	Shortbill spearfish.	15.0	Cape Kumukahi, Hawaii.
August 26, 1965	[2] 12.2	do	13.2	Waianae, Oahu.
Do	13.1	Blue marlin	72.6	Do.
October 6, 1965	17.8	do	49.4	Do.
October 18, 1965	[2] 19.8	Striped marlin	36.7	Ilio Pt., Molokai.
October 28, 1965	16.7	do	22.2	Cape Kumukahi, Hawaii.
November 4, 1965	[2] 12.1	Shortbill spearfish.	5.4	Do.
November 8, 1965	17.4	Striped marlin	33.6	Do.
November 10, 1965	25.0	do	36.7	483 km. south of Oahu.
November 12, 1965	[2] 16.4	do	29.0	Waianae, Oahu.
December 20, 1965	[2] 18.1	Blue marlin	42.6	Do.
January 20, 1966	28.9	Striped marlin	39.0	Do.

[1] Data from Yoshida (1965).
[2] Estimated from regressions.

AGE AND GROWTH

Because the juvenile albacore were collected from the stomachs of billfishes, any size selectivity by the billfishes could affect the analysis of the growth rate of the juveniles. Bias could be introduced by interspecific and intraspecific differences in the size of juveniles eaten by billfishes (e. g., larger billfish preying on larger juveniles). It is possible that billfishes do not feed on small juveniles. Fish shorter than 7 cm. SL were not found in the stomachs of the billfishes.

Other factors that may affect the estimation of growth are (1) changes in spawning season from year to year (the data for all years were pooled), (2) individual variation in growth, and (3) size-associated differences in schooling behavior and distribution of juvenile albacore so that the entire size range of juvenile fish would not be available to the predators. These factors are probably only a few of the many that may affect the data. I assume that all these factors have not seriously biased the data and that the juveniles eaten by billfishes are fairly representative of the population.

The standard length of the juvenile albacore is plotted against sampling date in figure 1. As would be expected, a considerable amount of variation in the size of juveniles is evident, particularly between August and November. Despite the scatter of the points, an increase in size with time is evident. A test showed that a second-degree polynomial provided a better fit to the data than a linear regression ($\underline{F}=7.491^{*}; d.f.=1, 32$). It was decided, however, to use the simpler linear regression because of the possible heterogeneity of the data, as discussed above. For example, most of the larger juveniles were found in striped marlin stomachs.

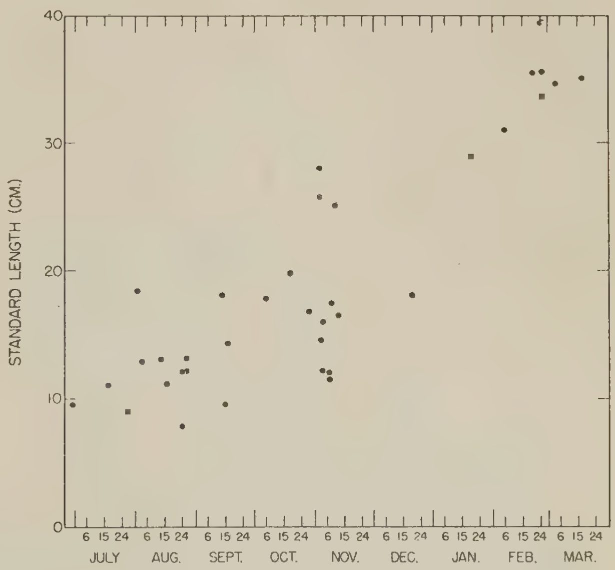

Figure 1.—The size and sampling date of juvenile albacore found in billfish stomachs.

For an initial approximation of the growth of the juveniles, a linear regression was fitted to the data with the hatching date set arbitrarily on April 1. Then, assuming a hatching size of 3 mm.,[3] I extrapolated the regression to obtain a better estimate of the hatching date, which proved to be in early May. The regression was then recalculated with May 1 as the hatching date. The linear growth is represented by

$$l = 0.349248 + 0.104184T$$

where l is standard length (cm.) and T is age in days. Figure 2 shows the regression and the observed data. Table 3 gives estimated lengths at various ages.

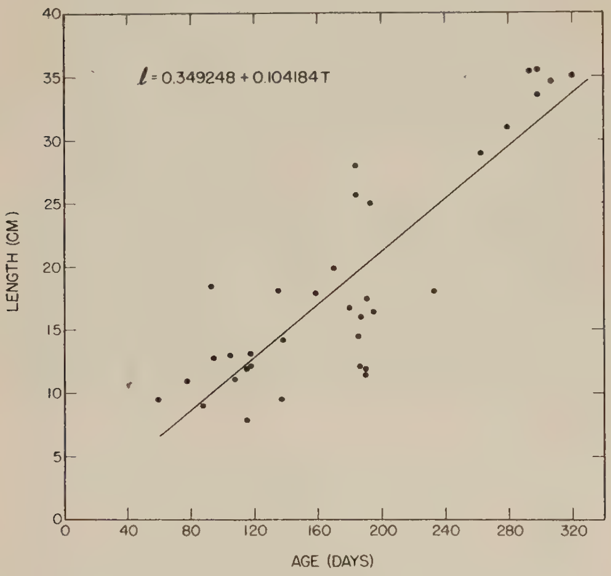

FIGURE 2.—Growth of juvenile albacore found in billfish stomachs.

TABLE 3.—*Expected lengths (derived from the linear regression) at various ages of juvenile albacore from billfish stomachs*

Age*	Standard length	Age*	Standard length
	Linear regression		Linear regression
Days	*Cm.*	*Days*	*Cm.*
60	6. 6	240	25. 3
90	9. 7	270	28. 5
120	12. 8	300	31. 6
150	16. 0	330	34. 7
180	19. 1	360	37. 8
210	22. 2	365	38. 4

*The age is based on an estimated hatching date of May 1 and should be considered only tentative.

The data from this study have a bearing on an unresolved problem in the biology of albacore—that of determining the absolute age of the fish. Various investigators, using scales and vertebrae for aging, have reported conflicting results in determining the absolute age of albacore. Others attempted to estimate the age of groups of albacore that appear regularly in the commercial catch. Investigators now generally agree that the modal groups in the Pacific albacore fisheries represent year classes, but disagree on the ages assigned to the year classes (Clemens, 1961; Otsu and Uchida, 1963).

The expected length that I estimated for 1-year-old fish is most similar to that given by Aikawa and Katō (1938), who made one of the earlier studies on the age and growth of albacore. Their results, however, were not generally accepted because they postulated rectilinear growth. Otsu (1960) was not entirely satisfied with the results of fitting a Gompertz curve to his growth data, which indicated that albacore required 3 years to grow about 30 cm. TL[4] (total length). In a later study Otsu and Uchida (1963) speculated that albacore 30 to 35 cm. TL, which sometimes appear in the commercial catches, were probably 1-year-old fish, and albacore 50 to 55 cm. TL were 2-year olds. Clemens (1961) and Bell (1962), on the other hand, assigned lengths of 52 cm. and 57.3 cm. TL, respectively, to 1-year-old albacore.

SEASONAL AND LENGTH DISTRIBUTION OF JUVENILE ALBACORE

Catch per unit of effort is often used to assess apparent abundance of fishes. For this study I used the number of juveniles per 100 billfishes as an index of apparent abundance. Juvenile albacore were found in stomachs of only three (striped marlin, blue marlin, and shortbill spearfish) of the five billfish species examined. In calculating the monthly apparent abundance of juveniles, however, I used the total of all billfish species for each month. I assumed that (1) no differences exist among the billfish species in relative efficiency in capturing prey and the apparent abundance of all the billfish species did not greatly change over the years and that (2) billfishes will feed on juvenile albacore when they are available, not selecting other prey in preference to juvenile albacore, or vice versa.

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[3] Matsumoto's (1958) observations suggest that tuna larvae are about 2 to 3 mm. long at hatching.

[4] Total length as defined by Marr and Schaefer (1949).

Serious error may result if my first assumption was not valid. Figure 3 shows the monthly distribution of striped marlin, blue marlin, and shortbill spearfish used in this study. These numbers generally reflect the seasonal abundance of these billfishes around Hawaii. Striped marlin are almost always more abundant than blue marlin and shortbill spearfish. Seasonally, striped marlin are most abundant from November to June and blue marlin are most abundant from June to September. Although the distribution of shortbill spearfish in figure 3 shows peaks in April and August, the seasonal abundance of this species is not well defined around Hawaii. Because of interspecific and intraspecific differences in seasonal abundance, differences in catching efficiency among the billfish species may affect estimates of juvenile albacore abundance. No attempt was made to test whether differences did exist in catching efficiency because the data were inadequate.

The second assumption is probably justified; studies on the food habits of billfishes indicate that they are broadly carnivorous (Royce, 1957).

Because of the small number of juveniles, the apparent abundance on a seasonal basis is shown in figure 4, for all years combined. Juvenile albacore occurred in billfish stomachs in all months except April and May; they were most numerous between August and November. The juveniles were generally larger in the winter than in the summer and fall. The large juveniles that were collected between January and March were most likely the progeny of spawning the previous spring.

My observations are consonant with the hypothesis of Otsu and Uchida (1963) that albacore spend their larval and early juvenile stages in subtropical waters and that the older juveniles then migrate into temperate waters. Otsu and Uchida also speculated that small albacore are probably abundant generally throughout temperate waters, but are not available to the commercial fisheries until they are 2 or 3 years old. Occasionally, small albacore (about 35 cm. TL) appear in the catches of the United States west coast and Japanese pole-and-line fisheries.

No attempt was made to find differences in abundance among areas, for example around the various islands, in Hawaiian waters. It is not realistic to do so because longline fishing is not random throughout the islands (Otsu, 1954). Because billfishes are fast-moving and can probably travel many miles in a single day, the location of their capture may not necessarily coincide with that at which they preyed on the juveniles.

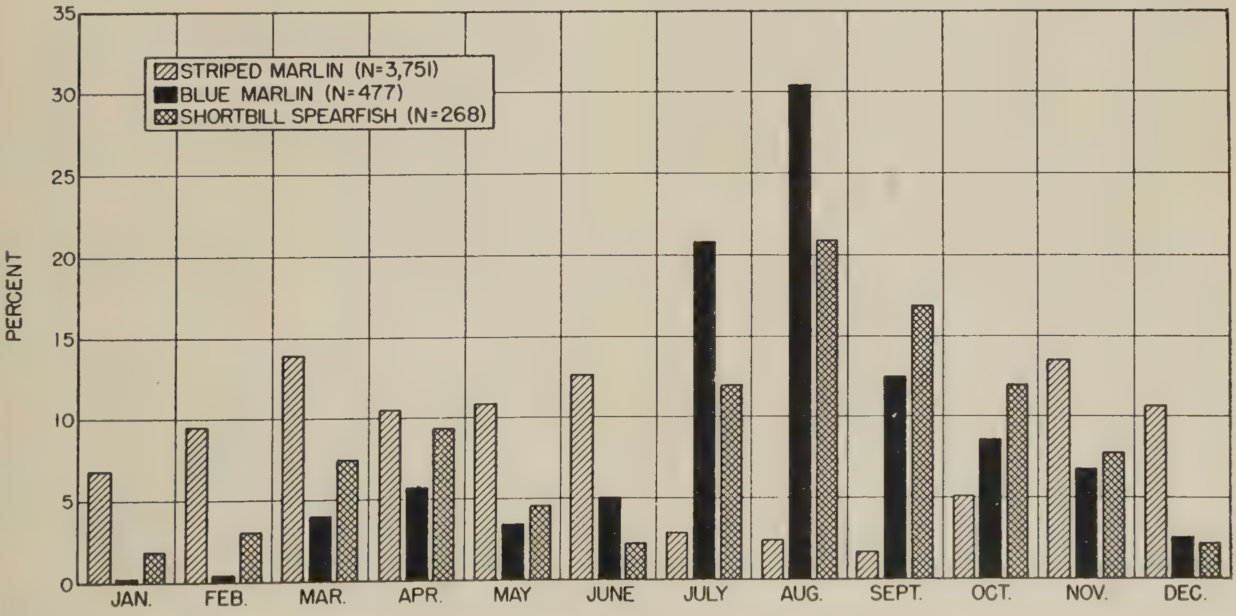

FIGURE 3.—Seasonal distribution of catches of striped marlin, blue marlin, and shortbill spearfish off Hawaii, 1962–65.

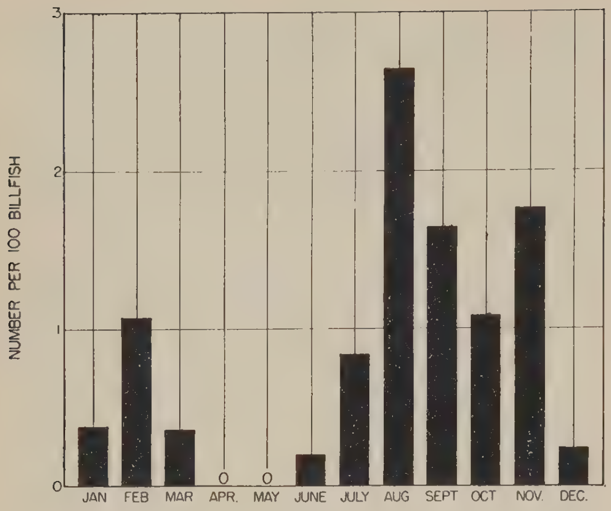

FIGURE 4.—Apparent seasonal abundance of juvenile albacore in Hawaiian waters, 1962–65.

SPAWNING

Yoshida (1965) reported that juvenile albacore occur near the Hawaiian Islands and tacitly assumed that albacore spawned in these waters. The most direct method of determining the spawning habits of fishes is to observe the spawning activity, where possible. Another method is to determine the seasonal and areal distribution of freshly fertilized ova and newly hatched larvae. Because these observations are not available, however, inferences on spawning must be made on indirect evidence.

Otsu and Uchida (1959), who examined albacore ovaries, indicated that albacore in the central and eastern North Pacific (between lat. 30° to 50° N. and the 180th meridian to the U.S. west coast) were either sexually immature fish or were adults that did not show signs of being near spawning. Adult albacore caught near Hawaii, however, showed evidence of active spawning during the summer. Furthermore, the northern limits of the distribution of all tuna larvae in the longitudes of the Hawaiian Islands are lat. 30° N. in the summer and 25° N. in the winter (Walter M. Matsumoto, personal communication). Finally, the wide size range of the juveniles around Hawaii suggests that they probably do not move great distances. I conclude, therefore, that albacore do spawn in Hawaiian waters and that the resulting juveniles spend at least part of their early life in these waters.

As noted earlier, the growth curve provided an estimate of early May as the time albacore larvae hatched. For all practical purposes the hatching and spawning periods can be considered coincident; Matsumoto (1958) estimated that the incubation period of fertilized tuna ova was not more than 4 days. The 5-percent confidence limits for the extrapolated hatching date suggest that albacore may spawn from March to September. I can conclude that albacore spawning around Hawaii peaks in May and may extend from March to September. These observations are not unlike that of Otsu and Uchida (1959), who postulated summer spawning for albacore in Hawaiian waters.

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SOME EFFECTS OF HYDRAULIC DREDGING AND COASTAL DEVELOPMENT IN BOCA CIEGA BAY, FLORIDA[1]

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ABSTRACT

Filling of 1,400 hectares (3,500 acres) of bay by hydraulic dredging has reduced the area of Boca Ciega Bay, Fla., by about 20 percent since 1950. An estimate of the annual standing crop destroyed is 1,133 metric tons (798 kg. per hectare, dry whole weight) of sea grass and about 1,812 metric tons (1,277 kg. per hectare, dry weight) of associated infauna. In terms of annual production, the loss of biological resources is far greater—minimum estimates are 25,841 metric tons of sea grass, 73 metric tons of fishery products, and 1,091 metric tons of infauna exclusive of meiofauna. Natural areas remaining in the Bay support local and offshore fisheries and are of value for recreation, public utilities, commerce, and industry. At an estimated value of $988 per hectare per year, worth of the estuarine area already eliminated is $1.4 million annually. In addition, inestimable secondary losses occur, principally from sedimentation, turbidity, and domestic sewage.

Boca Ciega Bay is a part of Tampa Bay, Fla., where coastal development and progressive deterioration of water quality have adversely influenced plant and animal production. This report describes some biological and physical changes that followed alteration of the bay and compares estuarine conditions in dredged areas with those in relatively undisturbed areas.

Hydraulic dredging became an accepted means of creating coastal upland in Florida about 1920, and has since proved an efficient means of providing waterfront real estate of premium value. Dredging was not a serious threat to coastal resources until after 1950 when coastal construction started on a large scale, especially along the lower east coast and the low-energy strand of the west coast from Tampa Bay southward. Profit and permissive attitudes toward the sale of submerged land contributed to rapid disposal of vast public holdings along much of Florida's 14,400 km. (9,000 statute miles) of tidal coastline. Bay filling has been little regulated, and in most situations biological and recreational resources of estuarine waters have been disregarded by coastal developers and governing authorities (Davis, 1956; Brunn and De Grove, 1959; Kidd, 1963).

Legislation to control dredge-fill projects in Florida appeared first in 1957 (Section 253.122 Florida Statutes, 1957), and the following year all such projects became subject to Federal review (Fish and Wildlife Coordination Act, P.L. 85–624). Unfortunately, under these laws the sale and development of submerged land remained largely arbitrary and most efforts to stop landfills in estuaries have been unsuccessful (Arnold, 1967).

Guidelines for appraisal of estuarine areas were proposed by Thompson (1961), and more positive measures are now being taken to conserve marine resources and provide for their rational use in Florida as well as in other parts of the country and abroad (Florida Statutes, chapter 67–393; Gilmour, 1965; Hutton, 1964; Tukey, 1965; Cain, 1966; Caldwell, 1966). Encouraging, too, is the

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fact that developers of bayfill projects have recently demonstrated a willingness to preserve some natural features on development sites (Gresham, 1967; Sykes, 1967).

In Florida and other States bordering the Gulf of Mexico, dredging and other forms of estuarine destruction damage fisheries because most of the species taken in sport and commercial fisheries live in estuaries during part or all of their life cycle (Skud and Wilson, 1960; Sykes and Finucane, 1966). Premium estuarine habitats that support the fisheries are vegetated, littoral biotopes containing populous, stable, and highly productive communities (Humm, 1956; Odum and Hoskin, 1958; Pomeroy, 1959; Odum, 1961; Margalef, 1963; Moore, 1963; Livingstone, 1965; Stephens, 1966; O'Gower and Wacasey, 1967).

Commercial fisheries in the Gulf of Mexico account for one-third of the Nation's marine landings and are worth about $114 million annually (Lyles, 1966). The landings could probably be increased two to five times through greater fishing effort, and use of species not now fished would raise these figures even higher (Schaefer, 1965; Pirie, 1967). In addition, production in some estuaries will certainly increase when methods are developed for culture of certain fishes, crustaceans, mollusks, and marine plants (Allen, 1963; Loosanoff and Davis, 1963; Shelbourne, 1964; Boney, 1965). Thus, perhaps the most timely argument against further destruction of estuarine habitats is the present and potential value of these areas for production of food (Tressler and Lemon, 1951; Hornig, 1966). Other nondestructive uses of estuaries, such as recreation, are compatible with fisheries and greatly add to the cash value of estuarine acreage, particularly in resort areas like Boca Ciega Bay.

DESCRIPTION OF AREA

Boca Ciega Bay lies within Tampa Bay, midway along the west coast of peninsular Florida. Separated from the Gulf of Mexico by a chain of barrier islands, Boca Ciega Bay merges with Tampa Bay on the south and extends 25.6 km. (16 miles) north as a narrow coastal lagoon (fig. 1). Water area is about 70 km.^{2} (27 square miles) and water depth over nearly 80 percent of the area is 1.8 m. or less (Olson, 1953; Olson and Morrill, 1955).

Bayfills occupy about 1,400 hectares (3,50 acres) and have reduced the water area by near 20 percent (Saloman, 1965). Aerial photograph taken before and after major dredging illustra how coastal development has reshaped Boca Cieg Bay in less than a generation (figs. 2–9).

In areas that remain relatively undisturbe sediments are a firm mixture of shell and san (Goodell and Gorsline, 1961). They support lux uriant beds of sea grass except in deep depression and channels where light is inadequate. Turtl grass (*Thalassia testudinum* König) is the mos common species, but in many places any of thre other species may be present (Phillips, 1960a 1962).

The first comprehensive study of Boca Ciega Bay began in 1955 as a joint project of the Florida Board of Conservation and the Fish and Wildlife Service (Hutton, Eldred, Woodburn, and Ingle 1956). The objectives were to determine commercial and recreational assets of the lagoon and focus attention on undesirable consequences of past and pending dredge-fill operations. Although the report did not impede bayfill construction, it described many biological and physical features of the bay. Subsequent work on the biology of Boca Ciega Bay included that of Springer and Woodburn (1960), Phillips (1960b), Dragovich and Kelly (1964), Saloman (1965), Sykes and Finucane (1966), and Bullock and Boss.[2]

PROCEDURE

Sampling began in September 1963 at 31 stations. Ten of these (BC series) had been previously sampled by biologists of the Florida State Board of Conservation (Hutton et al., 1956). The other 21 (D and PB series) were in natural areas, deeply dredged canals, and a variety of habitats influenced to some degree by dredging. On the basis of an evaluation of initial collections at all stations, we selected six (PB series) to represent conditions at dredged and undredged locations. Sampling at these stations began in November 1963 and continued at 3-month intervals for 9 months (February, May, and August 1964). Four stations (PB 1, 3, 5, and 6) were in undredged areas, and two (PB 2 and 4) were in dredged access canals be-

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[2] Bullock, Bob, and Chuck Boss. The ecological distribution of the marine mollusks in Boca Ciega Bay—1962. On file at Department of Biology, Florida Presbyterian College, St. Petersburg, Fla. 33711.

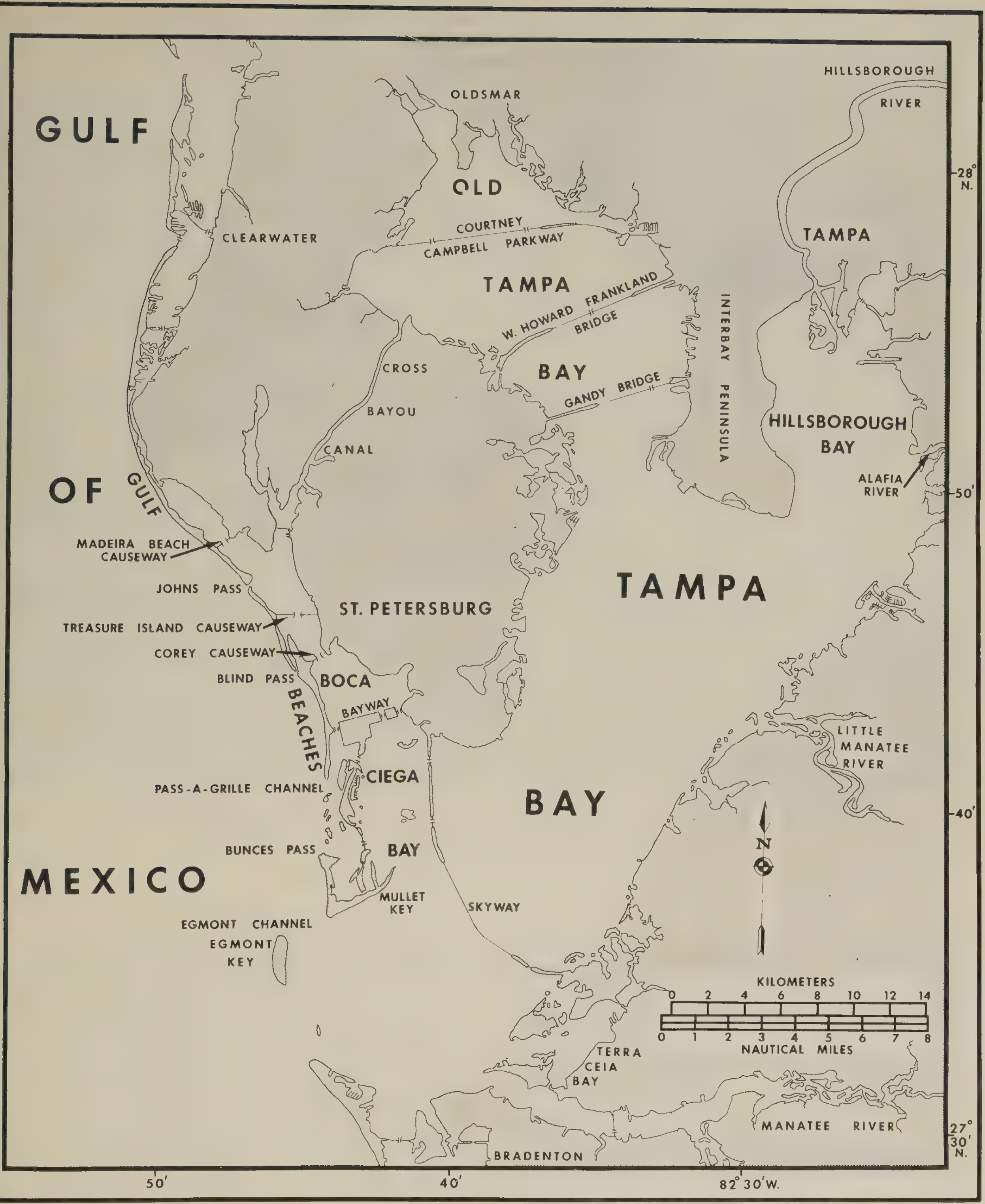
GULF OF MEXICO
GULF
OLDSMAR
HILLSBOROUGH RIVER
OLD TAMPA BAY
COURTNEY CAMPBELL PARKWAY
CLEARWATER
TAMPA
W. HOWARD FRANKLAND BRIDGE
INTERBAY PENINSULA
CROSS BAYOU CANAL
GANDY BRIDGE
HILLSBOROUGH BAY
ALAFIA RIVER
MADEIRA BEACH CAUSEWAY
JOHNS PASS
TREASURE ISLAND CAUSEWAY
COREY CAUSEWAY
BLIND PASS
ST. PETERSBURG
TAMPA BAY
BOCA CIEGA BAY
BAYWAY
BEACHES
PASS-A-GRILLE CHANNEL
LITTLE MANATEE RIVER
BUNCES PASS
MULLET KEY
SKYWAY
EGMONT CHANNEL
EGMONT KEY
N
KILOMETERS
0 2 4 6 8 10 12 14
0 1 2 3 4 5 6 7 8
NAUTICAL MILES
TERRA CEIA BAY
MANATEE RIVER
BRADENTON
28° N.
50'
40'
27° 30' N.
50'
40'
82° 30' W.

FIGURE 1.—Boca Ciega Bay and Tampa Bay, Fla.

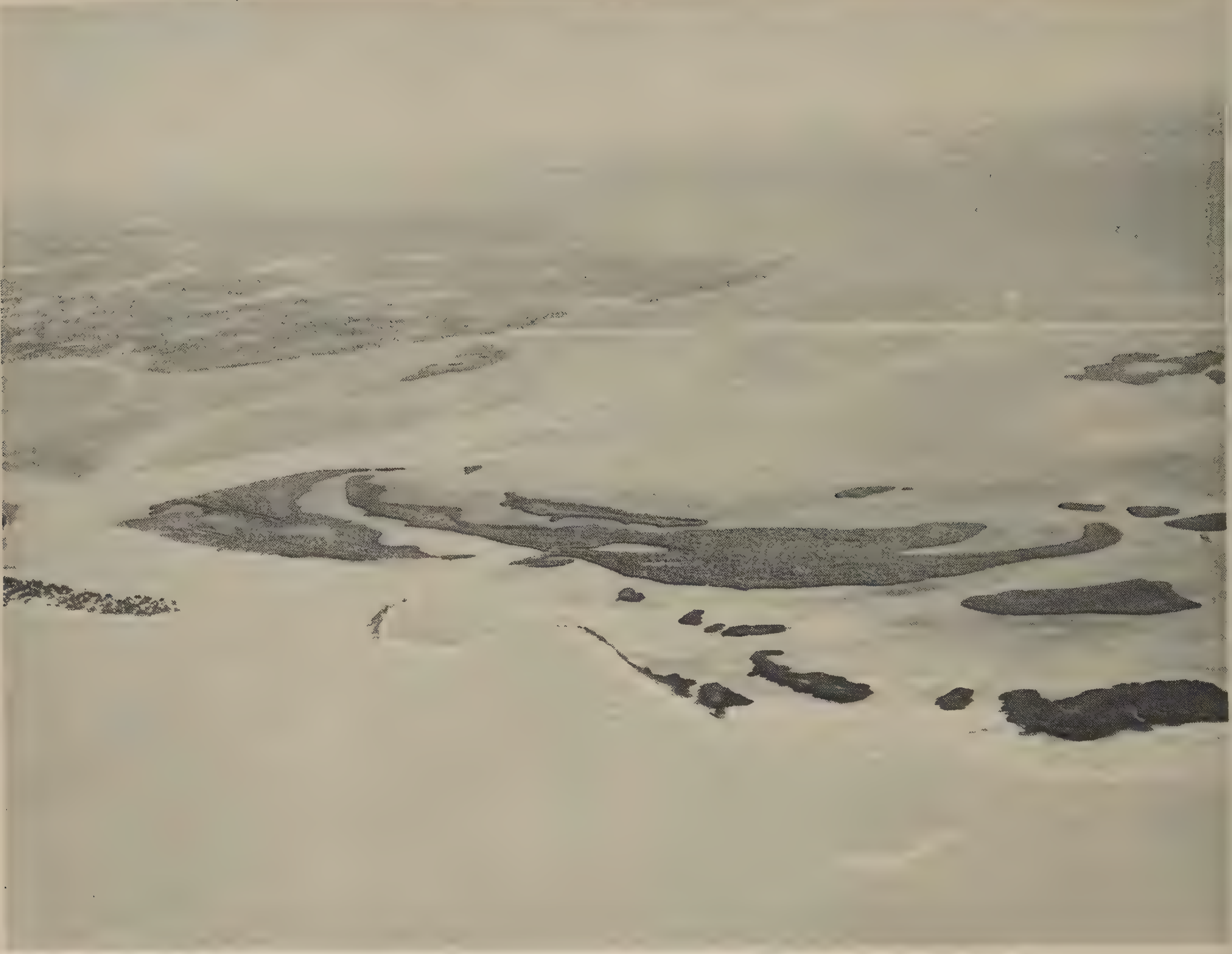

FIGURE 2.—Southern Boca Ciega Bay in 1953 before major bayfill construction (photograph courtesy of Airflite, St. Petersburg, Fla.).

tween bayfills. In addition, four areas of the bay (A, B, C, and D) were sampled in August 1964 to estimate the biomass of turtle grass and infauna (figs. 10 and 11). At all sampling stations, water was collected at surface and bottom for physical and chemical analyses, sediment samples were obtained for textural and chemical analyses, and biological collections were made for benthic invertebrates, plants, and fishes.

Measurements were made of water temperature, salinity, pH, total phosphorus, dissolved oxygen, secchi disc depth, chlorophyll *a*, and primary production following methods described by Saloman, Finucane, and Kelly (1964)—see table 1. Supplemental data on water quality were used to show long-term hydrological changes that have occurred throughout Tampa Bay as a result of coastal development (tables 2–5). The supplementary data are from the following published reports and unpublished data of the Bureau of Commercial Fisheries Biological Laboratory, St. Petersburg Beach, Fla.: Odum (1953), Hutton et al. (1956), Marshall (1956), Finucane and Dragovich (1959, 1966), Pomeroy (1960), Dragovich, Finucane, and May (1961), Saloman et al. (1964), Dragovich, Kelly, and Finucane (1966), Saloman and Taylor (1968), May and Johnson (unpublished data on

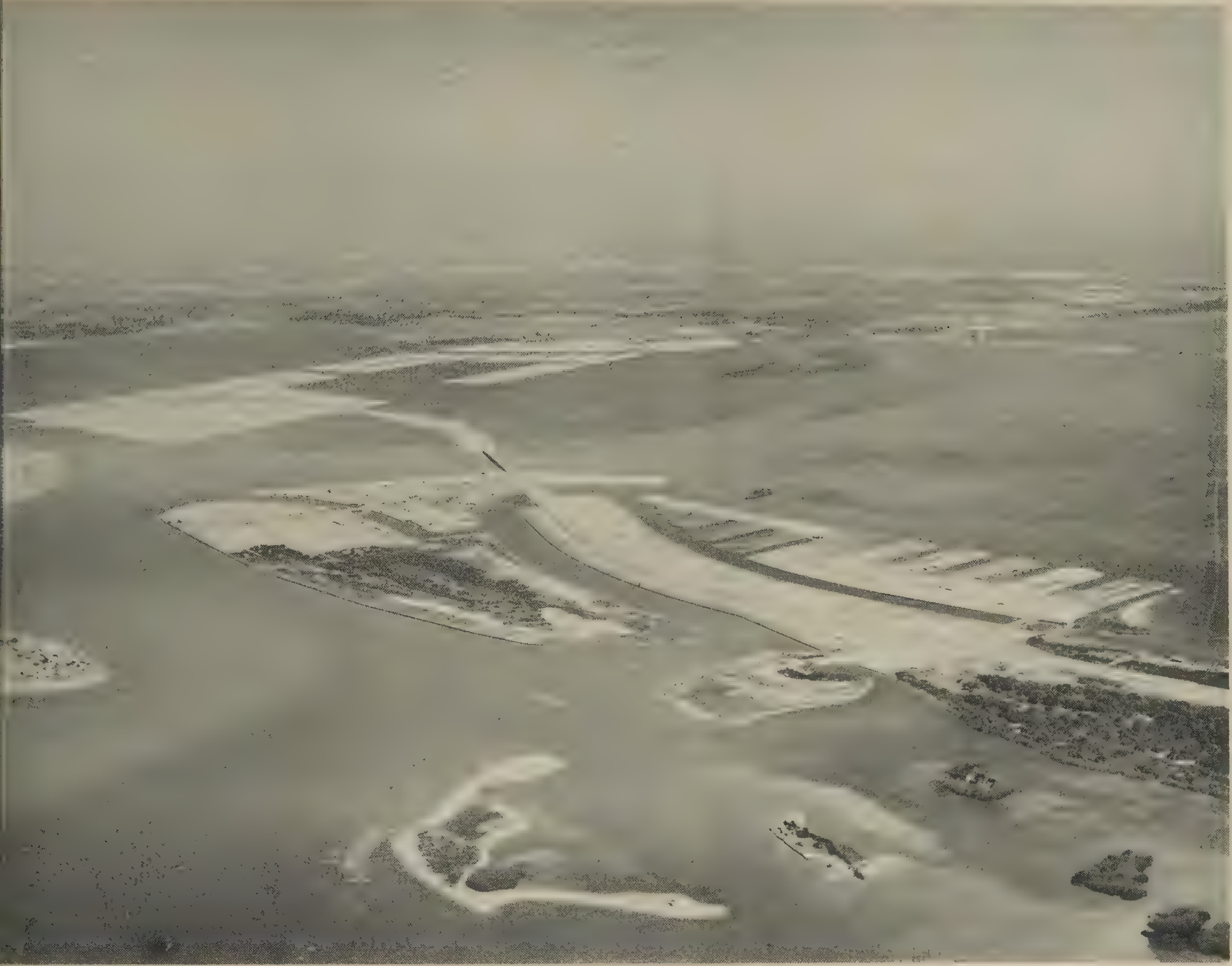

FIGURE 3.—Southern Boca Ciega Bay in 1963 showing Pinellas County Bayway and other bayfill areas (photograph courtesy of Airflite, St. Petersburg, Fla.

chlorophyll *a* and primary productivity),[3] and the U.S. Weather Bureau (unpublished water temperature data for Egmont Key).[4]

Sediments and infauna were collected with a shovel in water as deep as 1 m. and with a bucket dredge at greater depths (Taylor, 1965). A subsample of about 500 cc. was withdrawn from each bottom sample for sediment analysis. Each subsample was sealed in a moist condition and later analyzed at Florida State University.[5] Particles of sand size and larger were separated from silt and clay by wet sieving through a screen of 62-micron mesh. Material remaining on the sieve was dried and subdivided by use of a series of nested screens mounted on a mechanical shaker. The fine fraction that passed the 62-micron mesh was sized electronically in a Coulter counter.[6] Clay minerals were examined by X-ray diffraction, and chemical analyses were made for carbonates, organic carbon, and organic nitrogen. Statistical calculations were made by computer and included mean

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[3] May, B. Z., and Lucius Johnson. On file at Bureau of Commercial Fisheries Biological Laboratory, St. Petersburg Beach, Fla. 33706.

[4] On file at U.S. Weather Bureau, Tampa International Airport, Tampa, Fla. 33614.

[5] Sediment analyses were under the direction of H. Grant Goodell, Sedimentological Laboratory, Florida State University, Tallahassee, Fla. 32306.

[6] References to trade names in this publication do not imply endorsement of commercial products.

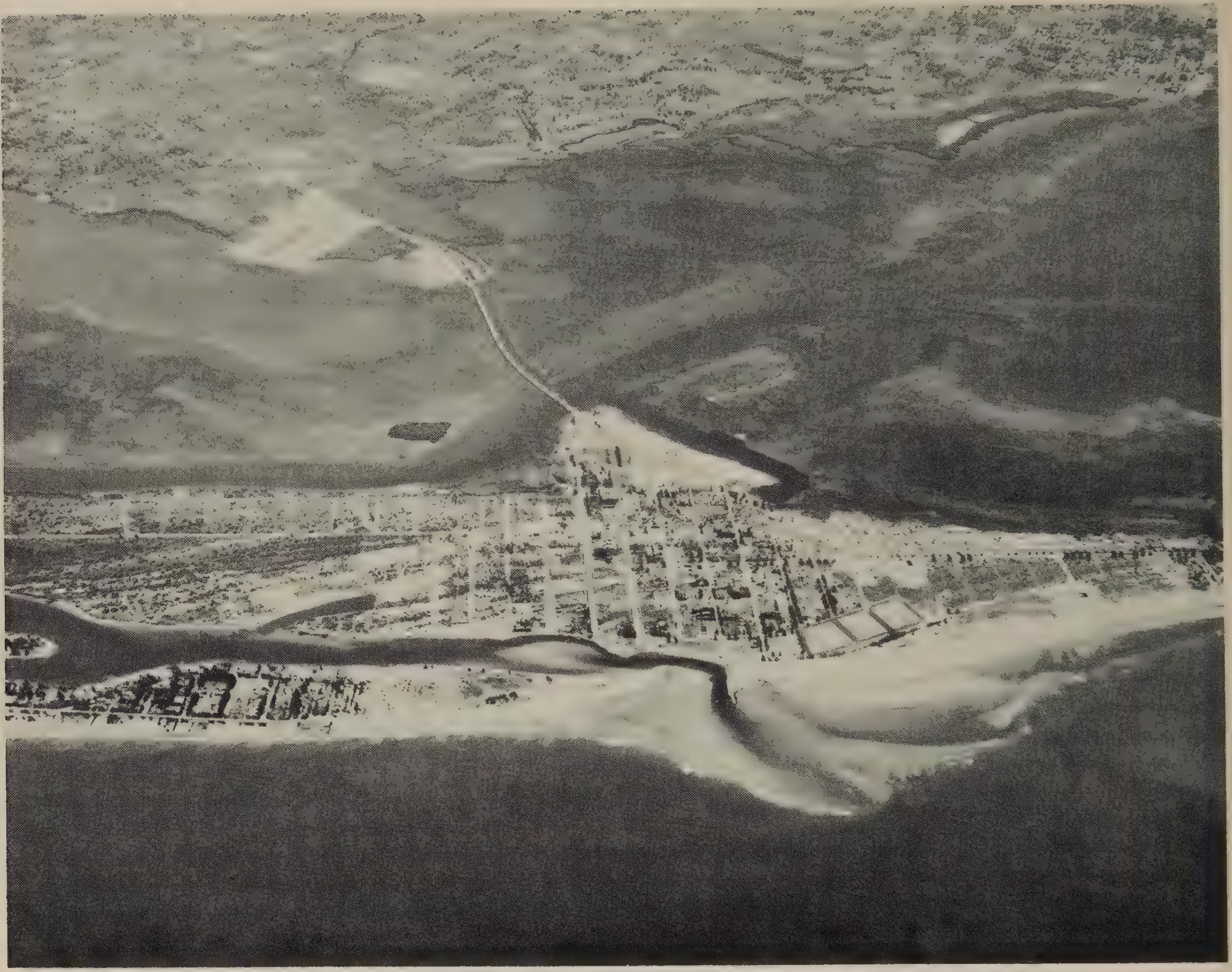

FIGURE 4.—Central Boca Ciega Bay near Corey Causeway in 1949 before major bayfill construction (photograph courtesy of Airflite, St. Petersburg, Fla.

grain size, standard deviation (sorting), skewness, and kurtosis.

In addition to the collection of bottom organisms taken by shovel and dredge, the epibenthos was sampled at all stations by a bottom drag fitted with fine netting (Taylor, 1965). Infauna was removed from sediments in a Tyler No. 24 screen of 30-cm. diameter and 0.701-mm. mesh. To distinguish small specimens from debris, rose bengal dye was added to material concentrated by screening (Jones, 1961). Ten percent sea-water Formalin used to fix specimens was replaced later by 70 percent isopropanol.

Fishes were collected at each station with either a 4.8-m. semi-balloon trawl or a 21-m. beach seine. The trawl was hung with a 3.75-cm. stretch mesh body fitted with a 1.25-cm. bag liner. The seine had a stretch mesh of 1.25 cm. in the end sections and 0.08 cm. in the bag. In addition, a 7.5-cm. stretch mesh trammel net, 90 m. x 1.8 m., was fished each sampling period at the entrance of access canals where stations were located. Fishes, invertebrates, and plants taken in nets and by bottom samplers were sorted, enumerated, and identified. Animals in each group are not treated in detail in the present report, although some are mentioned because of their prominence in bayfill canals.

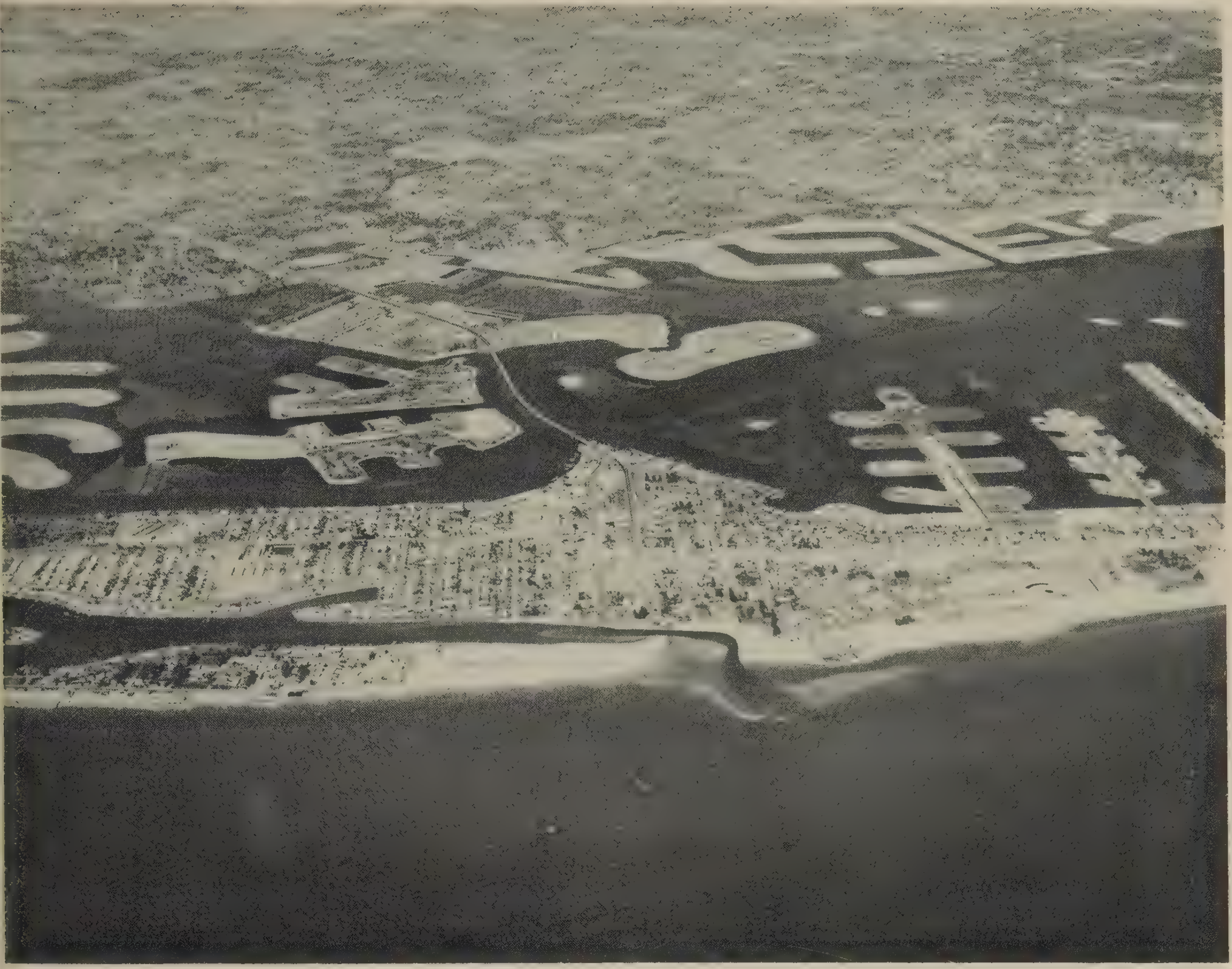

FIGURE 5.—Central Boca Ciega Bay near Corey Causeway in 1963 showing bayfill areas (photograph courtesy of Airflite, St. Petersburg, Fla.).

Quantitative samples for estimates of biomass were taken in August 1964 with a 0.25 m.^{2} plug sampler that extracts sediments to a depth of 22.5 cm. (fig. 12). In operation, the sampler is pushed into the sediment and then dug out with a shovel which covers the bottom of the sampler and retains the sediment plug. Total weights of plants and infauna from grass beds were determined from sets of triplicate samples taken in representative stands of turtle grass in lower, central, and upper Boca Ciega Bay (areas A, B, and C, fig. 10). Infaunal biomass from unvegetated bottom was determined from a single set of three samples in the central part of the bay shoreward of station D–5 in area D (fig. 11). Wet and oven-dried plants and wet whole animals were weighed on a Mettler K–7 balance. Dry whole weight of animals was arbitrarily calculated at 15 percent of wet whole weight because most of the animals in all samples were polychaete worms, small crustaceans, and small mollusks (Sanders, 1956; Thorson, 1957). Large mollusks and crustaceans that appeared sporadically in bottom samples were disregarded in calculations of standing crop because of the bias they would have introduced. Consequently, figures for dry whole weight of animals are conservative, particularly in lower Boca Ciega Bay (area A), where the southern hard-shell clam (*Mercenaria*

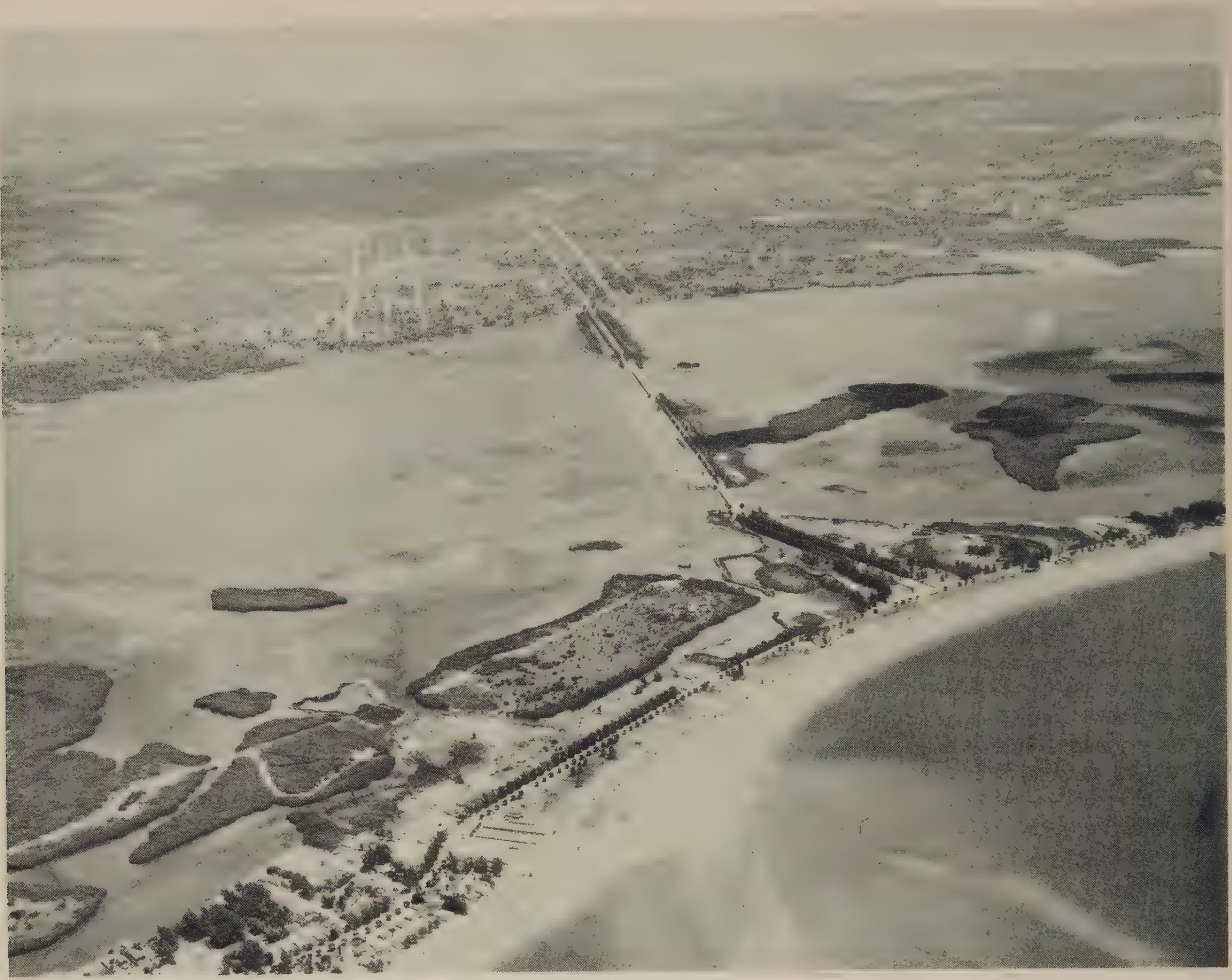

FIGURE 6.—Central Boca Ciega Bay near Treasure Island Causeway in 1949 before major bayfill construction (photograph courtesy of Airflite, St. Petersburg, Fla.

campechiensis) and pink shrimp (*Penaeus duorarum*) are abundant (Saloman, 1965; Taylor and Saloman, 1967). Biomass estimates of turtle grass are also minimal because the sampler did not collect roots and rhizomes that penetrate sediments beyond 22.5 cm. (9 inches).

TEMPERATURE, SALINITY, AND pH

Temperature, salinity, and pH of Boca Ciega Bay are similar to those in water near the mouth of Tampa Bay because land drainage is not appreciable and four passes lead directly to the Gulf of Mexico. Furthermore, there is little or no stratification of water masses in unprotected parts of the bay because of shallow depths and tidal and wind-driven circulation (table 1).

The most detailed record of water temperature for lower Tampa Bay comes from daily observations over 18 years by the U.S. Coast Guard at Egmont Key. The monthly means correspond closely to means of our water temperature data for 1963–64 and to means of other records from Boca Ciega Bay between 1961 and 1965 (tables 1 and 2). The range of water temperature over shallow flats, however, is considerably greater than the range of monthly means. For example, Phillips (1960b) recorded 36.9° C. from water standing over turtle grass in July 1958, and a low of 4.8° C.

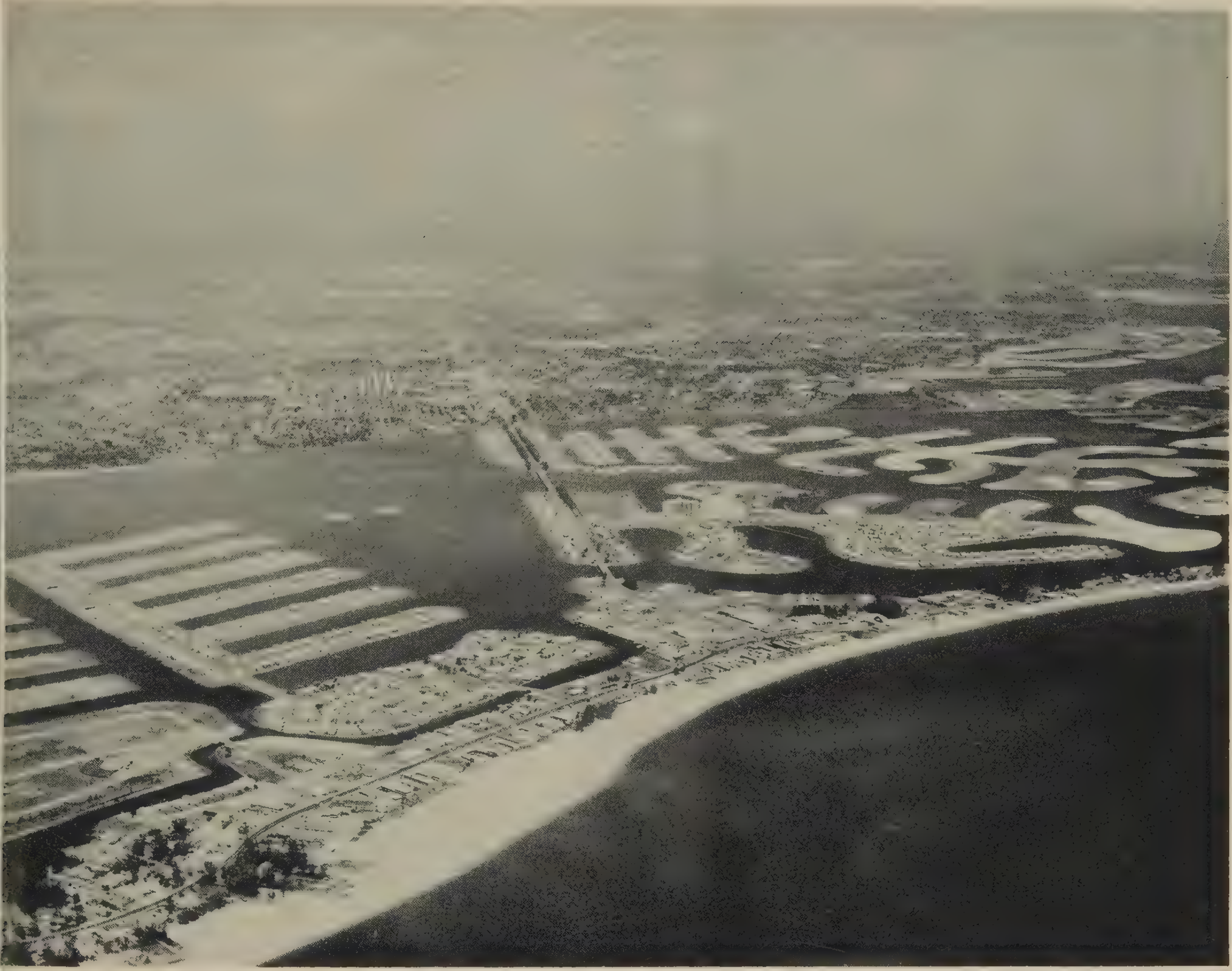

FIGURE 7.—Central Boca Ciega Bay near Treasure Island Causeway in 1963 showing bayfill areas (photograph courtesy of Airflite, St. Petersburg, Fla.).

was recorded near shore at Mullet Key on January 31, 1966 (Saloman and Taylor, 1968).

Water temperature is usually the same in the open bay and in bayfill canals, except in winter when periodic cold fronts create a temporary thermocline in deep water. At such times, bottom water may be 4 to 5° C. warmer than surface water and serves as a refuge for polythermal fishes (Kinne, 1963). If cold weather persists for more than a few days, however, bottom water becomes cold and sequestered fishes may die. During prolonged cold in February 1966, John H. Finucane (unpublished data)[7] observed mass mortality among snook, *Centropomus undecimalis* (Block), in bayfill canals of Boca Ciega Bay.

Average salinity in Boca Ciega Bay (32 p.p.t.) approaches that of the nearshore Gulf and is at least 10 p.p.t. higher than water in northern reaches of Old Tampa Bay and Hillsborough Bay (table 3). Even though the major portion of annual rainfall (127 cm.) comes in the summer and fall, seasonal fluctuations of salinity in the lagoon are slight. Appreciable changes occur only in surface water directly south of Lake Seminole Dam

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[7] Unpublished data (quarterly report) on file, Bureau of Commercial Fisheries Biological Laboratory, St. Petersburg Beach, Fla. 33706.

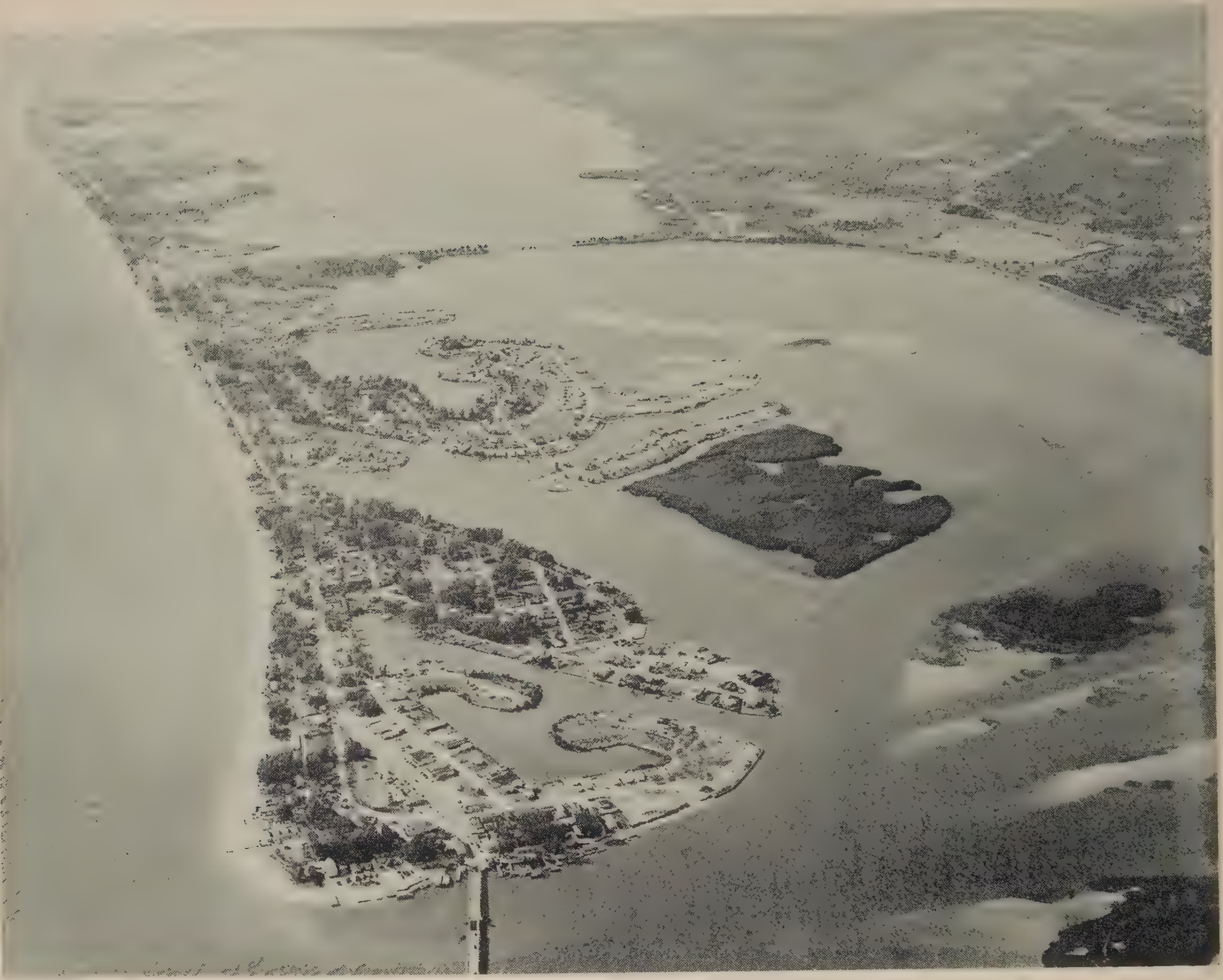

FIGURE 8.—Northern Boca Ciega Bay near Johns Pass in 1952 showing first bayfill areas (photograph courtesy of Airflite, St. Petersburg, Fla.).

at station PB–1 (fig. 10 and table 1). Stable and relatively high salinity in Boca Ciega Bay and the temperate or subtropical water temperature favor the occurrence of a large number and diversity of marine plants and animals (Gunter, 1961; Kinne, 1964).

In the sea, pH is generally near 8 and remains stable unless affected by abnormally high photosynthetic activity, rapid temperature change, or anoxic conditions on the sea floor (Skirrow, 1965). In Boca Ciega Bay the observed pH range of 7.2 to 8.5 is normal for water of nearly oceanic salinity (Park, Hood, and Odum, 1958; Reid, 1961). Within any single sampling period pH on the surface and bottom at each station varied no more than one unit.

OXYGEN

Daytime concentrations of oxygen on the surface and bottom of dredged and undredged stations were at least 3.5 ml./l. in all seasons (table 1). In more recent work, however, less than 2 ml./l. was recorded in June and August from bottom water at a dredged location in the central part of Boca Ciega Bay near station PB–4 (Dragovich et al., 1966). These recent data show that oxygen is re-

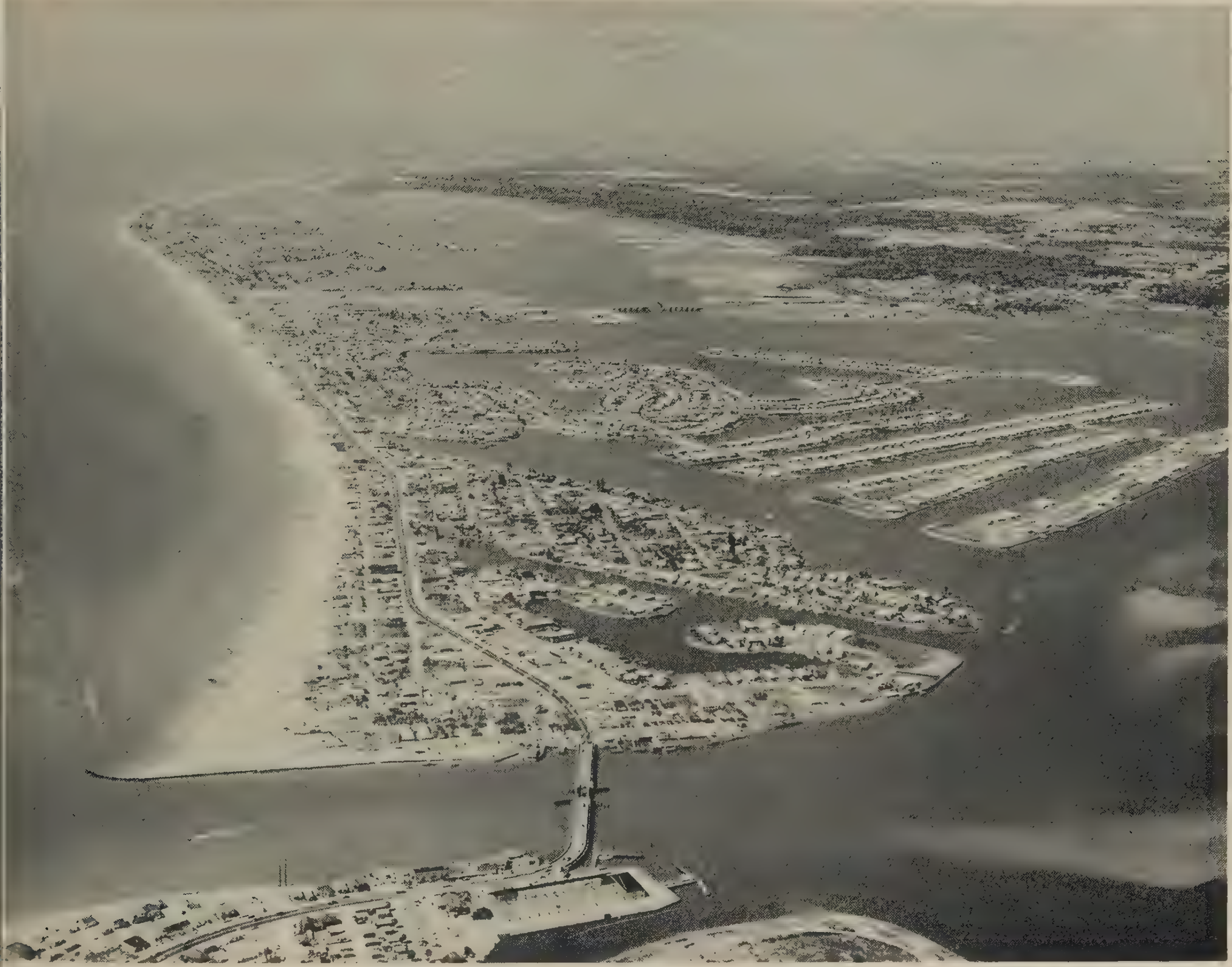

Figure 9.—Northern Boca Ciega Bay near Johns Pass in 1963 showing bayfill areas (photograph courtesy of Airflite. St. Petersburg, Fla.).

luced in summer over the soft sediments of access anals. Tidal movements in the bay probably make some oxygen available throughout the water olumn at most times, but occasional reductions imit some marine animals (Emery and Stevenson, 957; Reish, 1959).

Elsewhere in Tampa Bay, marked oxygen reduction near the bottom has been recorded only in Hillsborough Bay (Saloman et al., 1964), where ollution from sewage is heavy, summer water temerature is high, and water circulation is poor. dditional bayfill development in Boca Ciega ay would increase sewage volume, impede water irculation, and further reduce dissolved oxygen.

PHOSPHORUS AND NITROGEN

Phosphorus concentration was high in surface and bottom water at dredged and undredged locations. At dredged locations, bottom concentration was generally higher than surface concentration. At undredged locations, however, concentration did not vary consistently with water depth (table 6). Phosphorus was probably reduced in calm, surface water between finger-fills by deposition of sorbed phosphates bound to particles of silt and clay (Pomeroy, Smith, and Grant, 1965).

Nitrogen was not measured in this study, but other data show that it is plentiful in Boca Ciega Bay (table 4).

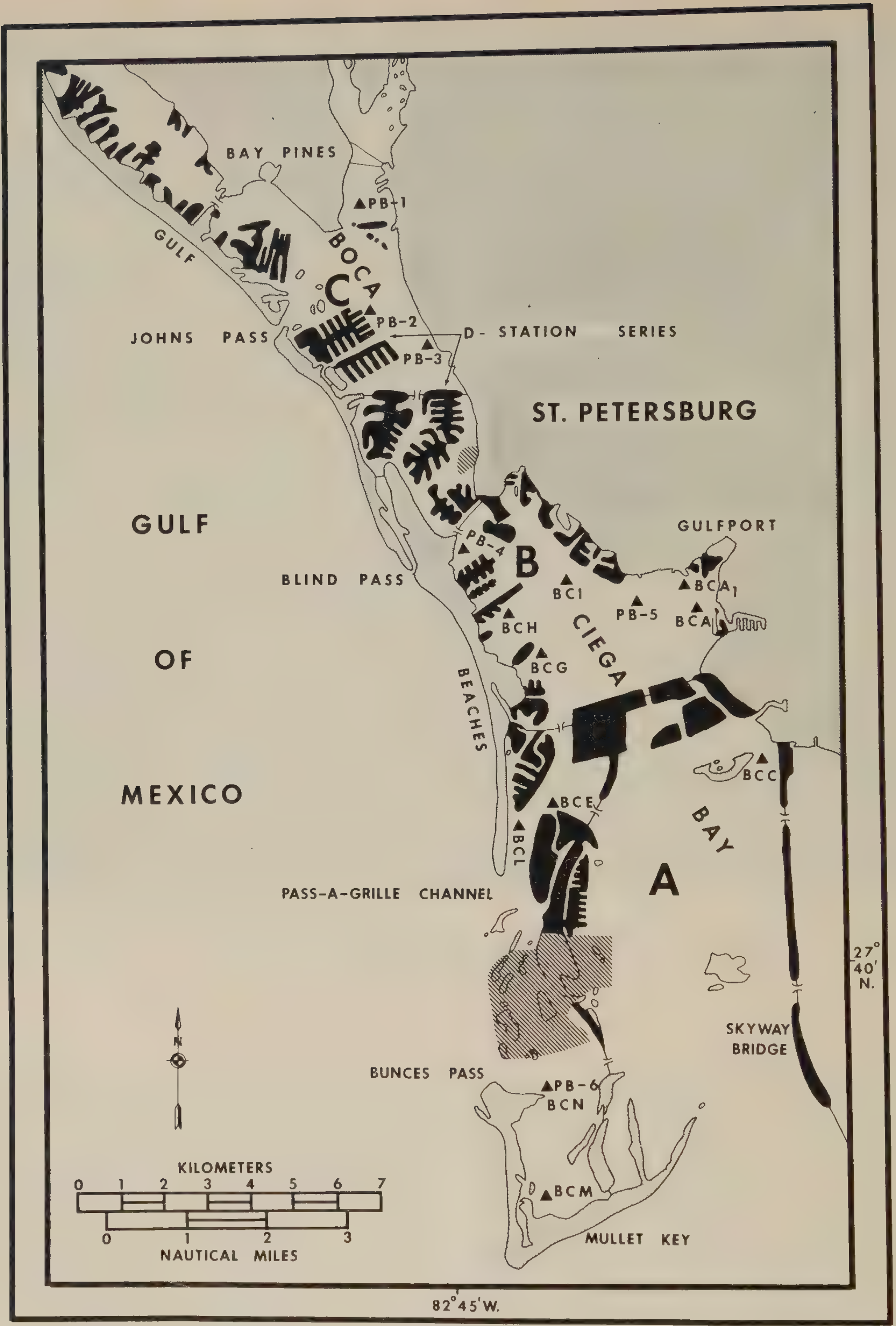
BAY PINES
PB-1
GULF
BOCA
C
PB-2
JOHNS PASS
D- STATION SERIES
PB-3
ST. PETERSBURG
GULF
GULFPORT
PB-4
B
BLIND PASS
BCI
BCA1
PB-5
BCA
BCH
CIEGA
BCG
OF
BEACHES
MEXICO
BCC
BCE
BAY
BCL
A
PASS-A-GRILLE CHANNEL
27° 40' N.
N
SKYWAY BRIDGE
BUNCES PASS
PB-6
BCN
KILOMETERS
0 1 2 3 4 5 6 7
BCM
0 1 2 3
NAUTICAL MILES
MULLET KEY
82°45'W.

Figure 10.—Boca Ciega Bay showing station locations (BC and PB series, and biomass stations A, B, and C), bayfill areas (black), and proposed bayfill areas (shaded).

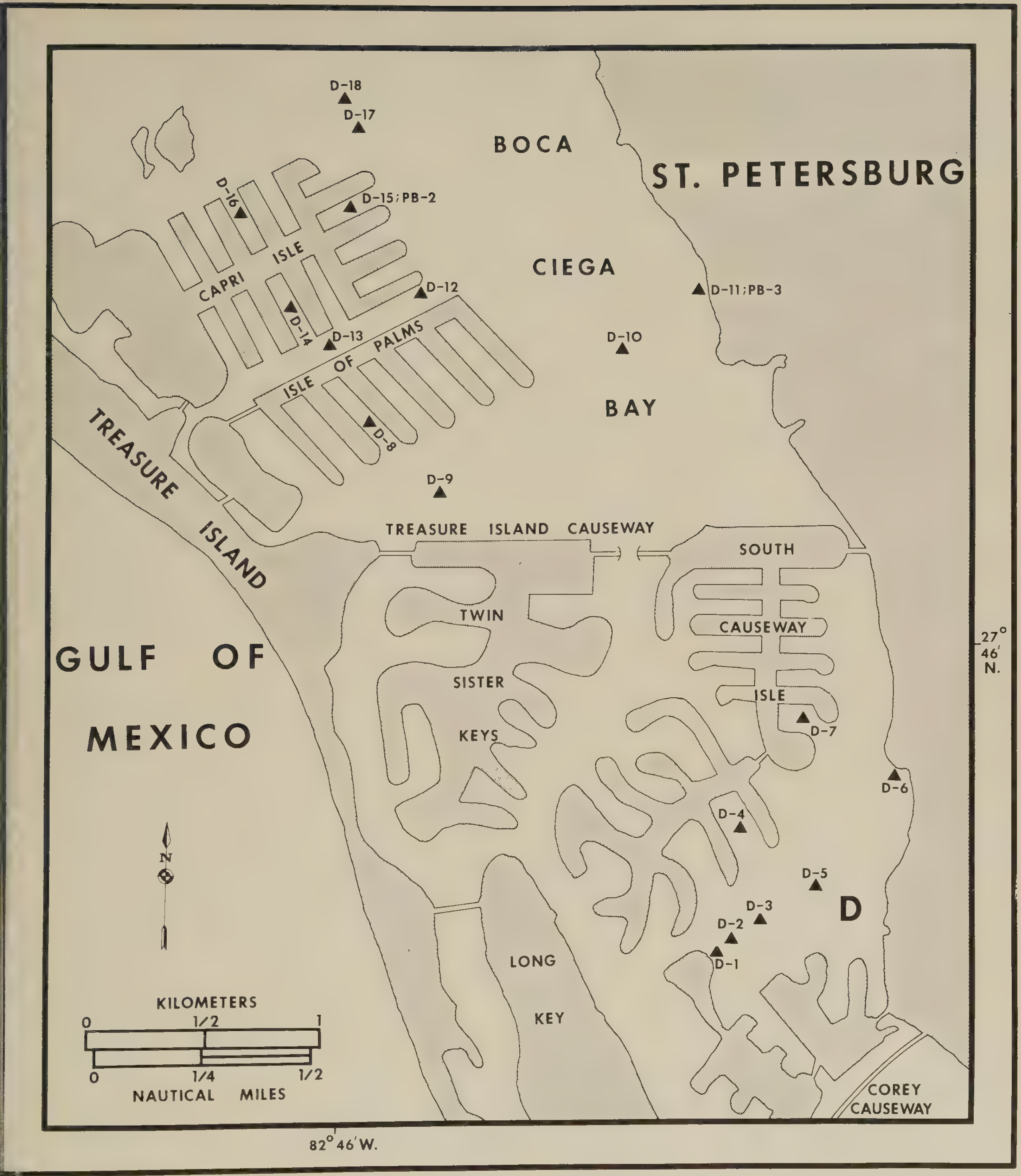
D-18
D-17
BOCA
ST. PETERSBURG
D-16
D-15; PB-2
CAPRI ISLE
CIEGA
D-12
D-11; PB-3
D-14
D-13
ISLE OF PALMS
D-10
BAY
TREASURE ISLAND
D-8
D-9
TREASURE ISLAND CAUSEWAY
SOUTH CAUSEWAY ISLE
TWIN SISTER KEYS
GULF OF MEXICO
27° 46′ N.
D-7
D-6
D-4
N
D-5
D-3
D
D-2
D-1
LONG KEY
KILOMETERS
0
1/2
1
0
1/4
1/2
NAUTICAL MILES
COREY CAUSEWAY
82° 46′ W.

FIGURE 11.—Boca Ciega Bay north of Corey Causeway showing station locations (D–1 through D–18, and biomass station D).

TABLE 1.—*Hydrological measurements from surface and bottom water at sampling stations in undredged and dredged areas of Boca Ciega Bay, Fla., 1963–64*

Date and stations	Depth	Temperature	Salinity	pH	Dissolved oxygen	Total phosphorus	Secchi disc depth	Chlorophyll *a*	Primary production
NOVEMBER 1963									
Undredged stations:									
PB-1	*M.*	*°C.*	*P.p.t.*		*Ml./l.*	*μg.at./l.*	*Cm.*	*Mg./m.³*	*G.C/m²/day*
Surface	0	20.9	29.6	8.0	4.6	16.6	105.0	13.1	0.52
Bottom	2	20.6	30.3	8.2	5.2	5.0			
PB-3									
Surface	0	19.8	31.9	8.2	4.7	22.1	100.0	11.1	.48
Bottom	2	19.4	31.9	8.2	5.5	21.4			
PB-5									
Surface	0	20.0	31.8	7.9	4.9	15.6	92.5	9.5	.44
Bottom	3	20.0	31.9	8.1	4.9	14.1			
PB-6									
Surface	0	20.5	32.5	8.1	5.3	1.1	240.0	1.5	.17
Bottom	4	20.4	32.8	8.0	5.2	17.3			
Mean surface value		20.3	31.5	8.1	4.9	13.9	134.4	8.8	.40
Mean bottom value		20.1	31.7	8.1	5.2	14.5			
Dredged stations:									
PB-2									
Surface	0	18.4	32.4	8.1	4.5	5.9	105.0	9.5	.37
Bottom	4	18.5	32.0	8.2	4.1	18.6			
PB-4									
Surface	0	19.8	31.7	8.0	4.4	4.7	130.0	12.9	.81
Bottom	4	19.7	31.7	8.0	4.0	1.1			
Mean surface value		19.1	32.1	8.1	4.5	5.3	118.0	11.2	.59
Mean bottom value		19.1	31.9	8.1	4.1	9.9			
FEBRUARY 1964									
Undredged stations:									
PB-1									
Surface	0	13.8	20.3	8.1	5.3	8.8	80.0	13.0	.44
Bottom	2	14.7	29.2	7.9	5.6	5.0			
PB-3									
Surface	0	15.2	29.7	8.5	7.8	3.8	92.5	4.6	.16
Bottom	2	13.9	31.0	7.8	6.1	3.9			
PB-5									
Surface	0	15.2	29.0	8.4	5.9	6.7	88.5	17.0	.25
Bottom	3	15.2	29.0	8.1	5.9	7.4			
PB-6									
Surface	0	14.7	31.6	8.1	5.4	6.4	112.5	13.3	.24
Bottom	4	14.6	31.7	7.2	5.4	7.1			
Mean surface value		14.7	27.7	8.3	6.1	6.4	93.1	12.0	.27
Mean bottom value		14.6	30.3	7.8	5.8	5.9			
Dredged stations:									
PB-2									
Surface	0	13.8	29.7	8.1	6.6	3.2	82.5	7.7	.27
Bottom	4	13.8	30.2	8.0	5.8	2.8			
PB-4									
Surface	0	14.7	28.2		5.9	5.4	82.5	18.9	.07
Bottom	4	14.5	28.8	8.1	5.3	5.4			
Mean surface value		14.3	29.0	8.1	6.3	4.3	82.5	13.3	.17
Mean bottom value		14.2	29.5	8.1	5.6	4.1			

TABLE 1.—*Hydrological measurements from surface and bottom water at sampling stations in undredged and dredged areas af Boca Ciega Bay, Fla., 1963–64*—Continued

Date and stations	Depth	Temperature	Salinity	pH	Dissolved oxygen	Total phosphorus	Secchi disc depth	Chlorophyll *a*	Primary production
MAY 1964	*M.*	*°C.*	*P.p.t.*		*Ml./l.*	*μg.at./l.*	*Cm.*	*Mg./m.³*	*G.C/m.²/day*
Undredged stations:									
PB-1									
Surface	0	27.0	33.6	7.8	3.6	6.1	87.5	9.9	.55
Bottom	2	26.8	33.4	8.0	3.8	6.2			
PB-3									
Surface	0	28.0	33.8	7.9	5.0	4.3	110.0	7.1	.48
Bottom	2	27.0	33.8	8.1	4.9	4.8			
PB-5									
Surface	0	27.9	32.9	7.9	4.1	12.4	115.0	3.5	.25
Bottom	3	27.7	32.9	7.9	3.9	10.9			
PB-6									
Surface	0	28.5	34.7		4.9	7.5	150.0	2.2	.19
Bottom	4	28.5	34.5	8.2	5.0	5.4			
Mean surface value		27.9	33.8	7.9	4.4	7.6	115.6	5.7	.37
Mean bottom value		27.5	33.7	8.1	4.4	6.8			
Dredged stations:									
PB-2									
Surface	0	27.3	34.0	8.0	4.5	4.1	142.5	6.6	.59
Bottom	4	26.6	34.1	8.3	4.0	4.9			
PB-4									
Surface	0	27.3	33.6		4.0	6.3	130.0		
Bottom	4	27.2	33.6		3.6	10.8			
Mean surface value		27.3	33.8	8.0	4.3	5.2	136.3	6.6	.59
Mean bottom value		26.9	33.9	8.3	3.8	7.9			
AUGUST 1964									
Undredged stations:									
PB-1									
Surface	0	29.8	27.7	7.8	4.5	15.8	45.0	28.2	.67
Bottom	2	27.7	31.8	7.9	3.8	11.8			
PB-3									
Surface	0	30.1	33.9	8.1	6.3	9.5	100.0	6.4	.33
Bottom	2	29.8	33.8	8.1	4.9	8.6			
PB-5									
Surface	0	30.5	33.3	7.4	4.8	12.9	125.0	4.5	.32
Bottom	3	30.0	33.3	8.4	4.8	13.3			
PB-6									
Surface	0	31.1	34.0	8.1	5.6	13.6	147.5	6.7	.59
Bottom	4	30.1	33.9	8.2	4.4	15.5			
Mean surface value		30.4	32.2	7.9	5.3	13.0	104.4	11.5	.48
Mean bottom value		29.4	33.2	8.2	4.5	12.3			
Dredged stations:									
PB-2									
Surface	0	30.7	34.3	7.9	5.2	7.1	105.0	10.6	.59
Bottom	4	29.8	34.4	7.9	3.5	7.2			
PB-4									
Surface	0	29.7	33.6	8.0	4.4		125.0	3.9	.28
Bottom	4	29.5	33.8	8.2	3.4	12.4			
Mean surface value		30.2	34.0	8.0	4.8	7.1	115.0	7.3	.44
Mean bottom value		29.7	34.1	8.1	3.5	10.8			

TABLE 2.—*Mean monthly surface water temperature (°C.) from observations (daily at 0700 hours) near Tampa Bay entrance (Egmont Key) 1948–65,*[1] *and Boca Ciega Bay (near station PB–4) 1961–65*[2]

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Egmont Key, Fla.:												
Mean low	13.9	12.7	16.3	20.0	25.1	27.5	27.9	28.5	27.0	24.0	19.4	14.6
Mean high	20.2	20.8	23.0	24.4	26.8	29.4	30.5	30.6	29.7	27.1	23.7	21.1
Mean	16.3	17.3	19.7	22.3	25.9	28.5	29.6	29.8	28.6	25.5	21.1	17.5
Boca Ciega Bay, Fla.:												
Mean	14.2	16.5	19.3	23.6	25.5	29.8	29.3	30.2	28.7	25.3	21.8	16.9

[1] U.S. Weather Bureau, Tampa International Airport, Tampa, Fla. 33614.

[2] Saloman et al., 1964; Dragovich et al., 1966; Finucane and Dragovich, 1966.

TABLE 3.—*Mean monthly surface water salinity (p.p.t.) for areas of Tampa Bay and adjacent Gulf of Mexico, 1954–65*[1]

Areas	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Yearly mean
Old Tampa Bay:													
Upper	20.0	18.6	21.1	23.5	22.8	26.4	22.5	22.6	18.3	21.4	21.4	23.1	21.8
Middle	23.4	21.8	22.3	23.8	24.9	26.5	25.8	22.3	21.6	21.4	22.4	23.7	23.3
Lower	25.8	25.8	25.3	25.8	26.9	27.6	26.9	24.6	22.6	23.8	23.7	24.7	25.3
Hillsborough Bay:													
Upper	19.7	22.2	19.3	22.8	19.8	23.6	19.3	19.1	16.6	21.3	22.3	23.0	20.8
Lower	21.3	21.2	21.4	22.3	21.3	25.9	23.6	20.4	22.0	22.9	25.2	25.6	22.8
Tampa Bay:													
Upper	25.6	24.6	22.7	23.0	25.9	27.5	26.5	22.0	21.2	22.7	24.8	25.8	24.4
Middle	27.5	26.8	25.0	25.0	28.1	29.0	29.0	23.4	24.3	25.8	26.5	27.5	26.5
Lower	30.5	29.3	28.5	30.6	31.4	31.8	32.2	30.3	29.1	29.8	30.5	30.7	30.4
Terra Ceia Bay	27.6	25.5	27.6	30.2	31.1	31.6	29.9	24.4	25.4	28.4	30.0	30.2	28.5
Egmont Key	31.9	31.9	31.5	31.5	33.1	34.1	34.3	32.4	30.7	31.0	31.7	31.8	32.2
Boca Ciega Bay	31.7	32.0	30.7	31.8	33.2	34.0	33.4	31.3	31.2	31.9	32.5	32.1	32.1
Gulf of Mexico	33.4	33.7	33.4	34.0	34.6	35.1	35.0	34.1	34.0	33.9	33.7	33.7	34.1

[1] Finucane and Dragovich, 1959; Dragovich et al., 1961; Saloman et al., 1964; Finucane and Dragovich, 1966; Dragovich et al., 1966.

TABLE 4.—*Surface values of total phosphorus, 1952–66, total nitrogen, 1961–66,*[1] *and nitrogen-phosphorus ratio (N/P)* [2] *for areas of Tampa Bay, Fla.*

Area	1952–53	1954	1955	1956	1957	1958	1959	1960	1961		1962		1963		1964		1965		1966	
	P	P	P	P	P	P	P	P	N	P	N	P	N	P	N	P	N	P	N	P
					μg.at./l.															
Area I—Old Tampa Bay:																				
January											44.5	20.6	31.2	29.9	33.7		37.6	23.6	26.1	24.6
February											24.2	23.7	35.8	22.3	33.7	29.1			15.7	27.6
March											42.6	14.6	43.0	18.5	49.6	28.2			55.8	18.7
April	7.7										47.0	18.5	63.5	32.5	39.1	22.3			62.4	20.7
May											54.4	23.9	36.4	25.9	27.6	24.9			40.7	28.7
June											50.2	28.0	31.7	19.6	27.6				62.8	30.1
July											47.7	21.5	74.1	19.4	25.4				36.4	11.9
August											46.6	21.4	42.8	25.5	69.4	24.2	83.1	25.5	46.3	14.0
September	8.1								57.0	21.6	58.4	21.2	52.4	26.6	46.4	23.7	61.7	25.1	58.8	25.5
October									41.7	26.2	35.4	29.8	36.0	5.6	43.3		66.6	28.2	64.3	19.3
November									38.9	18.5	27.2	30.9			33.6	24.6	47.9	22.1	48.4	18.3
December									39.4	22.3	62.2	23.2	31.8	18.5	28.0	21.6	46.1	22.1	47.5	19.3
Yearly mean	7.9								44.3	22.2	45.0	23.1	43.5	22.2	38.1	24.8	57.2	24.4	47.1	21.6
N/P									.9		.9		.9		.6		1.3		1.0	
Area II—Hillsborough Bay:																				
January													37.9	36.1	48.1					
February													55.3	25.5	50.7					
March													57.0	23.5	47.4					
April	18.7													27.9	60.7					

See footnotes at end of table.

TABLE 4.—*Surface values of total phosphorus, 1952–66, total nitrogen, 1961–66,*[1] *and nitrogen-phosphorus ratio (N/P)* [2] *for areas of Tampa Bay, Fla.*—Continued

Area	1952–53	1954	1955	1956	1957	1958	1959	1960	1961		1962		1963		1964		1965		1966	
	P	P	P	P	P	P	P	P	N	P	N	P	N	P	N	P	N	P	N	P
Area II—Hillsborough Bay—Continued																				
May													41.0	42.7	45.4					28.6
June													38.3	23.2	30.7					25.4
July													77.4	22.7	43.6					10.1
August													60.9	29.5	73.9				69.6	11.2
September	23.9										59.2	23.3	55.7	26.0	50.1				90.7	23.0
October											50.5	31.4	49.7	16.9	44.1				95.5	18.7
November											75.3	32.6			67.4				73.3	19.9
December											41.4	16.4	60.7	22.1	47.6				71.8	18.2
Yearly mean	21.3										56.6	25.9	53.4	26.9	50.8				80.2	19.4
N/P											1.0		.9						1.8	
Area III—Tampa Bay:																				
January								22.8		24.5	21.0	23.2	35.6	33.3					26.8	22.4
February								23.6		23.0			28.5	22.5					31.3	8.8
March								28.3			46.8	19.5	44.1	26.0	33.0				58.3	19.7
April	3.5							23.7			31.3	31.0	54.0	9.6	59.3				76.6	11.4
May								22.6				24.9	31.4	25.2	37.6				37.0	31.7
June								22.7		24.2	37.7	24.3	30.0	22.0					45.0	20.8
July								20.9		26.9	40.6	20.7	32.1	18.4	28.7				44.8	10.1
August								21.1			42.1	20.5	34.0	25.0	26.0		79.3	20.2	50.1	10.7
September	9.2							27.9	50.7	32.5	29.0	18.8		27.0	20.7		71.4	19.1	56.5	28.5
October									36.7	24.5	33.4	29.1	37.9	19.0	28.7		49.4	24.6	61.9	17.5
November								21.1	34.3	19.5	42.2	31.4			27.4		42.0	21.0	51.1	17.9
December								23.5	25.1	18.0	48.2	14.5	38.6	10.4	20.0		44.7	20.5	46.7	18.1
Yearly mean	6.4							23.5	36.7	24.1	37.2	23.4	36.6	22.6	31.3		57.4	21.1	48.8	18.1
N/P									.7		.7		.7				1.1		1.2	
Area IV—Tampa Bay Entrance:																				
January								2.1	26.9	7.7	33.3	10.9			26.1				14.7	6.2
February				13.6				3.9	18.1	4.7			22.0	10.6	21.2				13.0	5.5
March				9.7				8.4		3.9	45.4	3.0	20.5		19.4				44.0	15.2
April				4.9				3.9			31.2	8.6	29.4	8.6	12.8				42.0	13.7
May				1.7				3.6	19.6	5.2	36.7	4.5	23.6	7.1	28.7				34.0	8.6
June				9.8				4.9	47.3	5.1	26.8	7.7	27.1	8.8	11.7				47.6	13.9
July				5.4				4.6	34.2	2.8	24.9	8.2	32.6	9.6	39.0				37.8	10.4
August								4.4			36.3	12.5	22.0	10.6	23.1		32.7	11.4	39.4	10.3
September	4.2		21.6	15.9				6.4	39.0	5.7	23.2	9.2	33.7	14.4	22.8		62.6	11.3	51.6	17.4
October			18.3	9.5				10.5	46.4	16.2			28.0	11.6	17.6		37.9	10.6	62.3	17.3
November				12.7				6.3	36.2	13.4	28.0	14.3			21.0		53.1	5.6	44.8	15.0
December			4.0					3.6	25.3	13.6	34.4	7.0	28.6	7.9	13.7		32.7	5.8	47.7	12.0
Yearly mean	4.2		14.6	9.2				5.2	32.6	7.8	32.0	8.6	26.8	9.9	21.4		43.8	8.9	39.9	12.2
N/P									2.5		1.3		1.3				2.0		1.5	
Area V—Boca Ciega Bay:																				
January							1.4				27.6	3.3			23.3		42.1	3.9	25.1	6.7
February							4.1				22.8	3.3	36.8	4.7	26.7	1.5			39.1	4.4
March						2.2	3.9				37.2	3.2	29.7	11.8	26.4	7.9			60.7	9.1
April		2.4				2.2	4.4				28.7	4.9		13.2	14.7				50.1	6.0
May						2.5	4.1				47.4	2.0	26.1	4.4	50.3	11.4			36.4	15.1
June						3.7	5.8				39.4	10.6	33.3	10.1		11.2			64.8	10.2
July						2.6	5.3				40.7	7.8	32.6	13.4		16.0			31.4	11.2
August						2.8	5.4				32.8	9.7	25.7	11.4	63.9		51.9	15.4	48.1	11.4
September						3.7	7.0		57.4	8.6	38.6	14.4		9.0	29.9	13.4	42.1	10.1	47.2	15.3
October						1.5	5.9		39.0	11.3			39.4	18.1			55.1	14.3	49.6	14.2
November	.8					2.3	2.5		30.3	6.9	25.2	12.8	29.0	4.3		9.0	42.4	6.7	41.3	8.9
December						1.1	3.1		43.2	5.3	35.3	4.0	31.8	3.1		6.5	38.6	4.2	47.6	7.5
Yearly mean	.8	2.4				2.5	4.4		42.5	8.0	34.2	7.0	32.6	9.4	33.6	9.6	45.4	9.1	45.1	10.0
N/P									3.0		2.5		1.7		1.7		2.0		2.0	

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[1] Odum, 1953; Hutton et al., 1956; Finucane and Dragovich, 1959, 1966; Dragovich et al., 1961; Saloman et al., 1964; Dragovich et al., 1966; Saloman and Taylor, 1968.

[2] To calculate the nitrogen-phosphorus ratio, μg.at./l. values for nitrogen and phosphorus have been converted to parts per million (p.p.m.) by multiplying by 0.014 (nitrogen) and 0.031 (phosphorus).

TABLE 5.—*Surface values of chlorophyll a (mg./m.^{3}), 1952–66, and primary production (G. C/m.^{2}/day), 1962–66, for areas of Tampa Bay, Fla.*[1]

Area	1952–53		1958		1962		1963		1964		1965		1966	
	Chlor. *a*	Primary prod.	Chlor. *a*	Primary prod.	Chlor. *a*	Primary prod.	Chlor. *a*	Primary prod.	Chlor. *a*	Primary prod.	Chlor. *a*	Primary prod.	Chlor. *a*	Primary prod.
Area I—Old Tampa Bay:														
January	2.0						3.3	0.32			1.6	0.44	8.1	0.22
February							1.7	.11					3.5	.14
March							6.8	.72	4.0	0.34	2.4	.29	3.6	.16
April	3.1						9.4	.61	6.3	1.34	7.1	.81	5.0	.24
May	3.1						3.9	.54	3.7	.61	2.1	.35	9.8	.37
June							10.4	1.26	1.8	.29			5.0	.28
July							20.0	.90	5.3	.48			5.1	.22
August							8.9	.96	3.9	.32	26.6	1.26	7.7	.43
September	9.9				10.9		15.2	.56	2.6	.32	9.1	.52	5.0	.28
October					15.2	0.97	5.9	.51			8.9	.41	6.5	.46
November					5.0	.39			5.1	.45	11.8	.56	3.1	.17
December					6.4	.41			12.6	1.13	8.1	.30	5.2	.25
Yearly mean	4.5				9.4	.59	8.6	.65	5.0	.59	8.6	.55	5.6	.27
Area II—Hillsborough Bay:														
January	4.6						25.9	1.79			5.5			
February							9.3	.71				.77		
March							25.7	.57	8.3	.51	7.1			
April	4.6						4.7	.23	27.5	1.41	3.6	.79		
May	7.9						16.1	1.26	.8	.33	6.0	.43		
June							4.9	.25	1.6	.13		.99		
July							27.1	1.66	13.7	2.08				
August							35.4	1.49	26.5	1.43				
September	13.3				18.8		29.0	.79	16.2	.70				
October					10.2	.19	11.3	.77						
November					14.7	.95			4.9	.23				
December					16.0	.61			8.2	.62				
Yearly mean	7.6				14.9	.58	18.9	.95	12.0	.83	5.6	.75		
Area III—Tampa Bay:														
January							2.2	.53			1.0	.14	7.6	.26
February							10.4	.82					6.4	.26
March							5.7	.64	4.7	.54	5.5	.65	5.6	.26
April	6.9						11.5	.64	13.4	.62	5.4	.37	6.3	.31
May							4.4	.42	4.1	.43	3.1		4.1	.16
June							3.6	.21	.6	.30			5.3	.30
July							3.0	.19	10.6	.77			8.4	.36
August							3.9	.43	4.3	.37	10.8	.52	12.7	.65
September	9.3				7.5		9.2	.56	8.7	.50	22.4	.74		
October					5.0	0.57	5.1	.22			4.8	.22		
November					11.0	.73			3.7	.21	10.5	.52		
December					3.0	.31	7.6	.59	2.6	.16	10.7	.44		
Yearly mean	8.1				6.6	.53	6.1	.48	5.9	.43	8.3	.45	7.1	.32
Area IV—Tampa Bay Entrance:														
January	1.7										2.2	.30	1.2	.04
February							2.8	.32					3.3	.14
March							1.6	.21	1.7	.38	3.9	.66	2.3	.10
April							1.9	.27	3.0	.54	2.4	.36	1.4	.07
May	3.1						6.1	.69	.7	.23	1.2	.10	2.5	.11
June							9.3	.54	.4	.07			2.6	.10
July							3.3	.47	2.9	.14			8.4	.40
August							2.8	.28	3.1	.31			6.9	.35
September	10.0				1.6		6.0	.75	5.3	.79	9.9	.52	8.2	.46
October					8.2	.57	1.9	.25			8.9	.37	21.1	.95
November					5.0	.49			11.4	.57	3.2	.15	5.9	.22
December					5.7	.41	3.8	.16	.7	.12	6.4	.26		
Yearly mean	4.9				5.1	.49	4.0	.39	3.2	.35	4.8	.34	5.8	.27

See footnote at end of table

TABLE 5.—*Surface values of chlorophyll a (mg./m.³), 1952–66, and primary production (G.C/m.²/day), 1962–66, for areas of Tampa Bay, Fla.*[1]—Continued

Area	1952–53		1958		1962		1963		1964		1965		1966	
	Chlor. *a*	Primary prod.	Chlor. *a*	Primary prod.	Chlor. *a*	Primary prod.	Chlor. *a*	Primary prod.	Chlor. *a*	Primary prod.	Chlor. *a*	Primary prod.	Chlor. *a*	Primary prod.
Area V—Boca Ciega Bay:														
January							7.5	.30	11.1	.47			9.1	.30
February							7.9	.27	7.4	.32			1.8	.07
March							6.2	.30	7.9	.41			19.3	.89
April	5.1						3.8	.28	4.5	.30			13.8	.67
May	3.4						5.0	.34	3.4	.22			4.7	.18
June					9.0	.71	6.5	.37	3.9	.25			15.8	.89
July			3.5		8.3	.51	7.6	.43					10.6	.45
August					8.7	.44	6.2	.36					9.2	.53
September					9.0	.44	10.0	.46			5.1	.26	8.1	.47
October					8.8	.47	5.0	.27			10.1	.41	11.6	.61
November	3.1				9.2	.40	6.7	.31			9.0	.41	5.5	.31
December					7.4	.32	9.5	.40			15.0	.59	7.1	.41
Yearly mean	3.9		3.5		8.6	.47	6.8	.34	6.4	.33	9.8	.42	9.7	.48

[1] Marshall, 1956; Pomeroy, 1960; May and Johnson, unpublished data, on file at Bureau of Commercial Fisheries Biological Laboratory, St. Petersburg Beach, Fla.; Saloman et al., 1964; Finucane and Dragovich, 1966; Dragovich et al., 1966; Saloman and Taylor, 1968.

Compared with average concentrations of phosphorus and nitrogen in surface sea water, Boca Ciega Bay has about five times more phosphorus and four times as much nitrogen (Sverdrup, Johnson, and Fleming, 1942; Armstrong, 1965; Vaccaro, 1965). Even when compared with other estuarine systems of the Atlantic and Gulf Coasts, Boca Ciega Bay and the other areas of Tampa Bay rank high in these elements (Newcombe and Brust, 1940; Williams, 1954; Riley and Conover, 1956; NcNulty, Reynolds, and Miller, 1959; Lackey, 1963; Mackenthun, 1965; Saville, 1966).

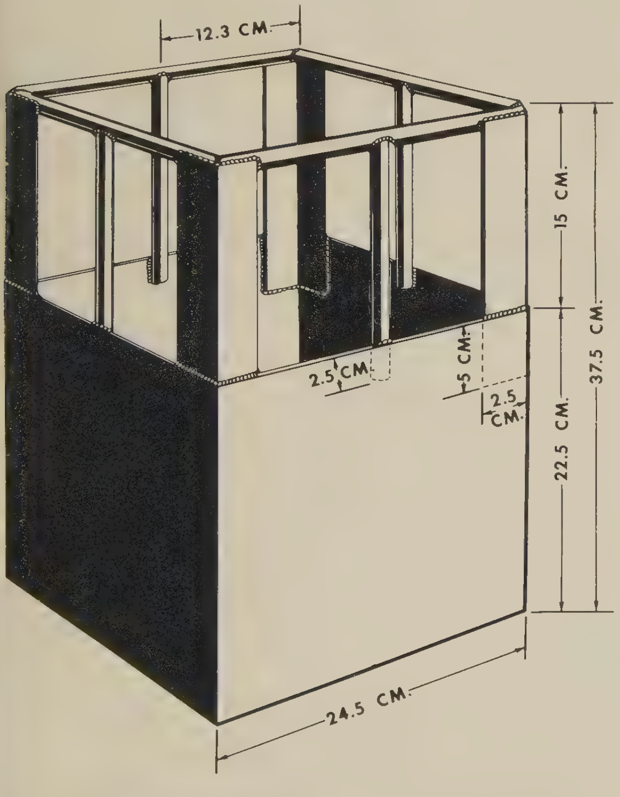

FIGURE 12.—Bottom sampler of stainless steel (0.25 m.²) used for sampling vegetation and infauna.

Under natural conditions, phosphorus and nitrogen enter Tampa Bay mainly through discharge from rivers and springs (Dragovich and May, 1962; Dragovich, Kelly, and Goodell, 1968). The major contribution of phosphorus enters Hillsborough Bay through the Alafia River from mining operations in extensive phosphatic deposits east of Tampa. On the basis of water analyses made in the early 1950's phosphorus in Hillsborough

TABLE 6.—*Mean total phosphorus from surface and bottom water of undredged and dredged sampling stations in Boca Ciega Bay, Fla., 1963–64*

	Undredged		Dredged	
	Surface	Bottom	Surface	Bottom
1963	*µg.at./l.*			
November	13.9	14.5	5.3	9.9
1964				
February	6.4	5.9	4.3	4.1
May	7.6	6.8	5.2	7.9
August	13.0	12.3	7.1	10.8
Mean	10.2	9.9	5.5	8.2

Bay has remained at about its present level since 1952 or before (Odum, 1953)—see table 4. In areas of the estuary less affected by mining runoff, high concentrations of phosphorus and nitrogen recorded since the early 1960's are due to an increase in industrial and domestic sewage. Population in the area around Tampa Bay was less than one-half million in 1950, rose to about three-fourths million by 1960, and is now near 1 million. As population rose, the method of sewage disposal was converted from septic tanks to treatment plant in the late 1950's and early 1960's. This change introduced treated sewage directly into all areas of the estuary. In Boca Ciega Bay, the mean annual concentration of total phosphorus rose from 2.5 μg.a./l. in 1954–58 to 4.4 in 1959, and 8 by 1961. At present, total phosphorus averages 10 μg.a./l. and total nitrogen 45.1 μg.a./l., and sewage volume is about 17 million gallons per day (secondary treatment) from outfalls located throughout the lagoon. Along with progressive eutrophication of Boca Ciega Bay, counts of coliform bacteria have risen so high that shellfishing has been prohibited near all outfalls and in all waters of the bay north of Pinellas County Bayway (fig. 13)—Pinellas County Health Department, personal communication.

Relative as well as total concentration of nitrogen and phosphorus influences the occurrence and abundance of marine life (Raymont, 1963). Within limiting values, studies of marine plankton indicate that growth and reproduction of marine phytoplankton are greatest when the ratio of nitrogen to phosphorus is 10 or higher (Odum, Lackey, Hynes, and Marshal, 1955; Lackey, 1963). In Boca Ciega Bay the observed N/P is about 2. The disproportionately high level of phosphorus may limit kinds and numbers of phytoplankton in the lagoon and perhaps explains why plankton blooms are infrequent and planktonic primary production is not extremely high (Dragovich, Kelly, and Kelly, 1965; Rounsefell and Dragovich, 1966; Dragovich and Johnson, 1966).

Attached algae and sea grasses also respond to eutrophy. McNulty (1961) noted an abundance of *Gracilaria blodgettii* Harvey, other red algae, and the green alga *Ulva lactuca* Linnaeus in Biscayne Bay, Fla., before pollution abatement. Wilkinson (1964) found a direct relation between eutrophication of a New Zealand estuary and marked increase of two green algae, *Ulva* sp. and *Enteromorpha* sp. He wrote that foul odor of hydrogen sulphide was emitted from decay of algal mats and that white paint was turned black on homes nearby. Production of hydrogen sulphide by *Enteromorpha* has also been studied by Baas Becking and Mackay (1956).

Species of *Gracilaria* have been implicated in reports of offensive odors arising from Hillsborough Bay (Florida State Board of Health, 1964). The Federal Water Pollution Control Administration is now investigating this matter. In Boca Ciega Bay, *Gracilaria* is present, as are *Ulva* and *Enteromorpha*. We observed windrows of *Ulva lactuca* in bayfill access canals after residents reported objectionable odors in the central part of the bay in the spring of 1965. Further nutrification of Boca Ciega Bay would increase growth of these and perhaps other filamentous algae that become fetid as they decompose.

TURBIDITY

Data from 1963–64 show that secchi discs were visible to depths greater than 150 cm. only in southern Boca Ciega Bay (PB–6), well away from bayfill developments (table 1). Here, average light transmission through the water column is 53 percent of incident radiation at about 40 cm. beneath the surface (Saloman et al., 1964). In contrast, water in the open bay nearer bayfills is turbid. Within protected waters of access canals, however, transparency approaches that of the lower bay. For example, average monthly light transmission in one canal was 45 percent at 40 cm. (Saloman et al., 1964). Even so, canal bottoms are far too deep to receive light required for the growth of sea grass.

Much of the silt and clay raised by dredging will eventually be removed from circulation in the lagoon by biological fixation and tidal transport (Dapples, 1942; Ginsburg and Lowenstam, 1958; Van Stratten and Kuenen, 1958; Phillips, 1960a; Lyntz, 1966). Until water is clarified by these processes, turbidity will continue to limit biological production in central and northern parts of Boca Ciega Bay.

CHLOROPHYLL *A* AND PRIMARY PRODUCTION

Neither chlorophyll *a* nor rate of planktonic primary production differed consistently in

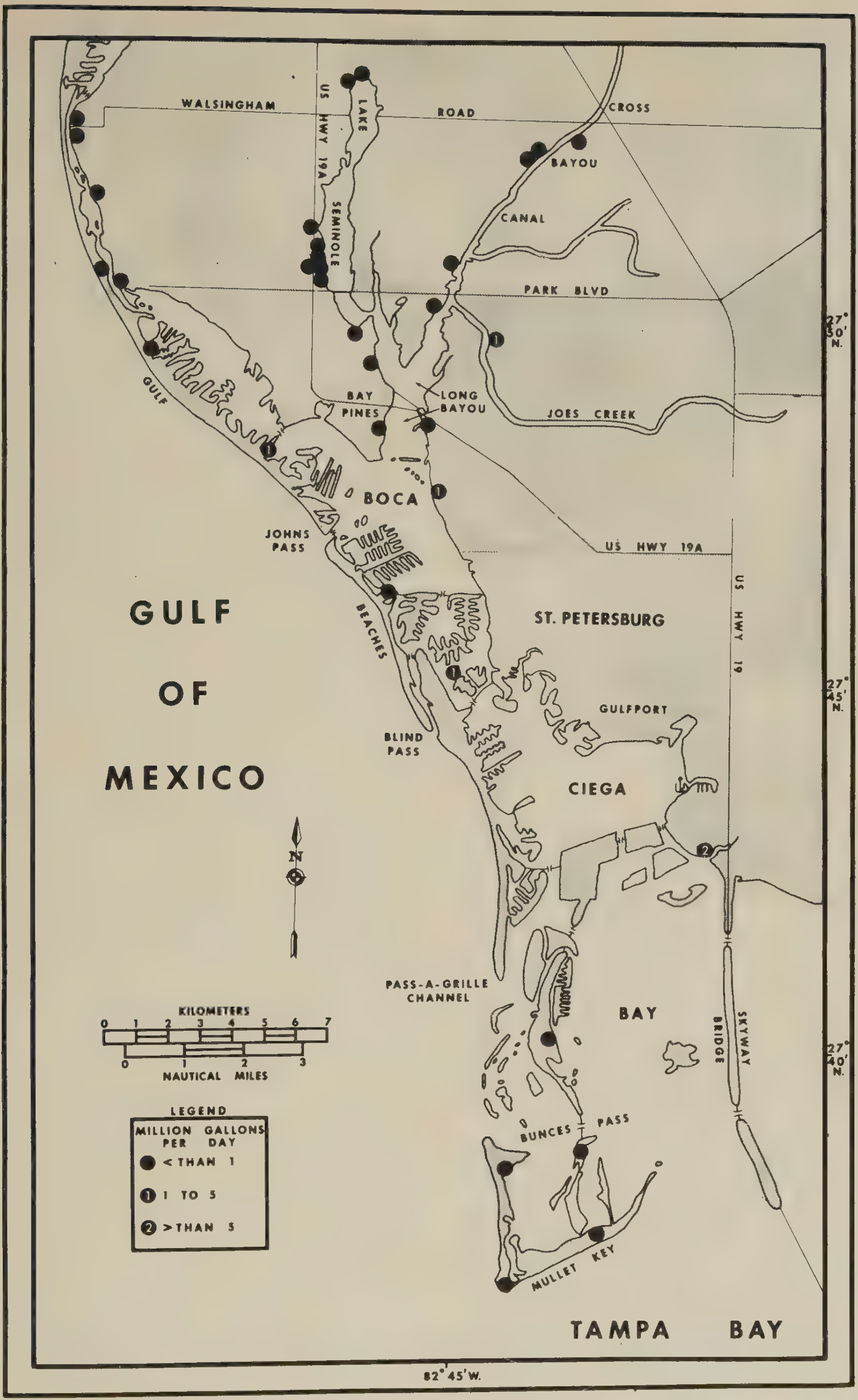
WALSINGHAM
ROAD
CROSS
BAYOU
CANAL
US HWY 19A
LAKE
SEMINOLE
PARK BLVD
27° 50' N.
GULF
BAY PINES
LONG BAYOU
JOES CREEK
BOCA
JOHNS PASS
US HWY 19A
BEACHES
ST. PETERSBURG
US HWY 19
27° 45' N.
GULF OF MEXICO
GULFPORT
BLIND PASS
CIEGA
N
PASS-A-GRILLE CHANNEL
BAY
SKYWAY BRIDGE
27° 40' N.
KILOMETERS
0 1 2 3 4 5 6 7
0 1 2 3
NAUTICAL MILES
LEGEND
MILLION GALLONS PER DAY
● < THAN 1
① 1 TO 5
② > THAN 5
BUNCES PASS
MULLET KEY
TAMPA BAY
82° 45' W.

Figure 13.—Approximate sewer outfall locations and discharge volumes (secondary treatment) in Boca Ciega Bay, Fla. 1966.

dredged and undredged locations. Chlorophyll *a* did not fluctuate seasonally. Low primary production noted in February may be due to turbid conditions rather than lack of nutrients or limitation by another factor, such as temperature (table 1). Except for higher values in extremely eutrophic Hillsborough Bay, pigment and production figures (table 5) are both similar to those recorded for other areas of the estuary as well as other estuarine waters of the southeast (Ragotzkie, 1959; Odum and Wilson, 1962; Williams, Murdock, and Thomas, 1966; Saville, 1966; Dragovich and Johnson, 1966).

In 1962–66, mean chlorophyll *a* in Boca Ciega Bay was 8.6 mg./m.^{3} and mean primary production by phytoplankton was 0.40 G.C/m.^{2}/day. The most extensive data for chlorophyll *a* and primary production in Boca Ciega Bay are from daily observations by May and Johnson[8] between June 1962 and June 1964 (table 5). These figures show a slightly lower mean annual value for chlorophyll *a* (7.3 mg./m.^{3}) but the same value for mean annual production (0.40 G.C/m.^{2}/day). Earlier data indicate about a twofold rise in chlorophyll *a* since 1952, following nutrification of the lagoon by sewage (table 5).

Actually, the productivity figures given above for Boca Ciega Bay are misleading and far too low because sea grasses and unicellular and filamentous benthic algae add to the production that was recorded only for phytoplankton. Pomeroy (1960), who considered photosynthetic contributions by all hydrophytes in his study of primary production in lower Boca Ciega Bay, concluded that an average value is about 5 G.0_2/m.^{2}/day. Odum and Hoskin (1958) gave a value of about 5 grams of dry organic material per day. On the basis of an allowance of 0.5 G. of C for each gram of organic matter produced (May, 1966), this is equivalent to about 2.5 G.C/m.^{2}/day or nearly six times the estimates of daily production in the lagoon by phytoplankton alone. The main point to be made is that under natural conditions primary production from a variety of photosynthetic taxa far exceeds production in turbid waters where photosynthetic activity of benthic flora has been reduced or eliminated (Blinks, 1955; Odum, McConnell, and Abbott, 1958; Pomeroy, 1959).

SEDIMENTS

Sediments of Tampa Bay are mainly a firm mixture of sand and shell containing little silt or clay (Goodell and Gorsline, 1961). Soft deposits are localized in upper reaches of Old Tampa Bay, Hillsborough Bay, natural depressions, and dredged bottom of bayfill access canals, where the weight percentage of silts and clays may exceed 90 percent. In Boca Ciega Bay the sediments in undredged areas averaged 94 percent sand and shell whereas the sediments in dredged canals averaged 92 percent silt and clay (table 7).

The ooze measured in two dredged pockets between bayfill fingers extended downward to a depth of about 3.6 m. The upper 30 cm. was dark, semifluid, and sulphurous; below was an unconsolidated horizon of gray clay. The predominantly organic upper layer consists of decomposing detritus that accumulates in the canals. The origin of the underlying clay has not been determined, but it seems likely that a thick stratum of clay was uncovered in the dredging which extended some distance below a bay floor veneer of sand and shell. To judge from the uniformity of the viscous clay layer, this material was redeposited after dredging ceased and now lies too deep to be reworked by normal water movements. Clay settles out of suspension slowly and may form deposits to 364 m. or more beyond dredging sites (Phillips, 1960a; Mackin, 1961; Hellier and Kornicker, 1962; Odum, 1963; Woodburn, 1965). Thus, resident benthos far from fill and borrow areas may be suffocated by sedimentation from dredging operations.

MACROBIOTA

Analysis of biological samples in Boca Ciega Bay supplements earlier studies in undredged areas and contrasts these findings with a scarcity of macrobiota found in bayfill canals.

DIVERSITY AND ABUNDANCE

In the first comprehensive survey of Boca Ciega Bay, Hutton et al. (1956) recorded nearly 200 plant and animal species from marine and tidewater communities and presented fishery statistics that attest to the importance of commercial and sport species. Later a notable addition was made to the list of algal species by Phillips (1960b); Springer and Woodburn (1960) brought the list of fishes from Tampa Bay up to 108; and unpublished work by Bullock and Boss[9] increased the recorded number of mollusks in Boca Ciega Bay from 30 to 175. Nearly 700 species of marine plants and animals have been identified from our sampling in 1963–64 and from other work in the area. Among the major taxa are about 180 species of mollusks, 120 polychaete worms, 60 decapod crustaceans, 20 echinoderms, 110 fishes, and 200 plants.

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[8] See footnote 3.

Comparative records show that stations inside deeply dredged canals contain less than 20 percent of the species we recorded for the bay. If fishes are excluded from the species total, nearly 100 percent of the organisms recorded come from collections made outside dredged areas. Invertebrates collected in bayfill canals consisted of only a few polychaete worms, mollusks, blue crabs, and pink shrimp. We conclude, therefore, that soft deposits in the canals are in some way unsuitable for most bottom invertebrates found in other areas of the bay. Thorson (1957) and others have demonstrated that larvae of many benthic forms are sensitive to sediment composition and will not metamorphose from a planktonic stage until contact is made with suitable bottom. In 10 years, recolonization of canal sediments has been negligible and it appears doubtful that soft sediments of bayfill canals will

TABLE 7.—*Comparison of sediments at undredged and dredged stations in Boca Ciega Bay, Fla. (1963–64), showing depth, mean grain size, percentage of shell and sand by weight (particle size <4 Ø), percentage of silt and clay by weight (particle size >4 Ø), and percentage of total carbon by weight*

Station	Depth	Mean grain size	Percentage of shell and sand by weight	Percentage of silt and clay by weight	Percentage of total carbon by weight
Undredged:	*Meters*	*Phi units (Ø)* [1]	*Percent*	*Percent*	*Percent*
BCA	2	3.5	81	19	1.7
BCH	2	2.5	95	5	.5
BCC	1	2.5	96	4	.7
BCE	7	2.6	99	1	.2
BCG	1	2.3	97	3	.6
BCI	3	3.4	87	13	1.3
BCL	1	1.9	98	2	.6
BCM	2	3.0	95	5	.7
PB-6; BCN	3	1.4	98	2	.4
D-1	3	2.8	98	2	.4
D-2	1	2.5	98	2	.4
D-3	1	2.5	88	12	1.4
D-5	2	2.6	97	3	.8
D-6	1	2.8	96	4	.8
D-9	2	2.8	96	4	.5
D-10	2	3.0	89	11	1.0
PB-3; D-11	1	2.9	92	8	.4
D-17	2	2.8	96	4	.5
D-18	1	3.4	85	15	1.3
PB-1	2	2.6	99	1	.3
PB-5	3	2.5	98	2	.4
Means	2	2.7	94.2	5.8	.7
Dredged:					
BCH	3	7.1	12	88	4.6
D-4	4	6.5	6	94	.6
D-7	4	6.3	5	95	8.9
D-8 [2]	2	4.6	60	40	6.6
D-12 [2]	1	.8	99	1	.2
D-13 [3]	4	4.0	83	17	.9
D-14	4	7.0	7	93	3.8
PB-2; D-15	4	7.0	6	94	1.3
D-16	4	6.3	14	86	1.3
PB-4	4				
Means	3.9	6.7	8.3	91.7	3.4

[1] The phi unit is a logarithmic transformation of the Wentworth grade scale of particle size (Krumbein and Pettijohn, 1938).

[2] Berm of canal not included in calculation of mean.

[3] Transitional bottom not included in calculation of mean.

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[9] See footnote 2.

ever support a rich or diverse infauna. The existence of soft sediments does not necessarily preclude the presence of a diverse and abundant bottom fauna (Barnard and Hartman, 1959; Sanders, 1960), but where sediments are highly organic, deposition rapid, and dissolved oxygen low, the benthos is likely to be impoverished (Pratt, 1953; Bader, 1954; Reish, 1959; McNulty, Work, and Moore, 1962; McNulty, 1966).

Forty-nine species of fishes were caught at stations in dredged canals. None were demersal, and the absence of this type of fish in the catch may be due to lack of food organisms on and in bottom deposits. In contrast, 80 species of fish were collected at stations outside bayfill canals. Even though waters in the open bay accounted for a greater number of fish species, 30 percent more fish were netted within dredged canals. One species, the bay anchovy, *Anchoa mitchilli* (Valenciennes), was most common in the canal catch but the Cuban anchovy, *Anchoa cubana* (Poey), and the scaled sardine, *Harengula pensacolae* (Goode & Bean), were also abundant.

BIOMASS AND PRODUCTION

The major benthic habitats in Boca Ciega Bay are turtle grass beds, unvegetated bottom, and oyster reefs. All contain large numbers of species, but the grass bed community is outstanding because it is widespread and highly productive.

Extensive beds of turtle grass now exist only south and east of the Pinellas County Bayway (fig. 1). Poorer stands are located in central and northern parts of the bay, but only in very shallow water. Representative beds were sampled to compare standing crop in the relatively undisturbed southern section of the bay (area A) with that in extensively dredged central (area B) and northern (area C) sections (fig. 10). Dry whole weight of turtle grass in areas A, B, and C averaged 1,198, 1,008, and 320 g./m.^{2}, respectively. The figure for area C agrees with other biomass estimates of turtle grass in the Gulf of Mexico, but values from areas A and B are two to three times greater (Phillips, 1960a; Odum, 1963). Maximum development of turtle grass probably occurs in the Caribbean where Burkholder, Burkholder, and Rivero (1959) have observed stands having a biomass of 2,800 g./m.^{2} dry weight.

Pomeroy (1960) reported an average biomass of about 81 g./m.^{2} for turtle grass sampled randomly along a transect across lower Boca Ciega Bay. This figure seems low, but no doubt includes values from samples in some sparsely vegetated areas. Since bayfills cover bare and vegetated bottom, 80 g./m.^{2} is probably a reasonable factor for calculating total biomass of turtle grass that has been covered by bayfills in Boca Ciega Bay. Using 1,400 hectares (3,500 acres) as the filled area of the bay, we compute that standing crop of turtle grass buried by filling is at least 1,133 metric tons. If the area of bayfill canals and other borrow areas were included in this calculation, the figure would be nearly doubled.

Our estimate of total primary production in Boca Ciega Bay is based on work by Pomeroy (1960) and studies in vegetated Texas bays by Hellier (1962) and Odum and Wilson (1962). An average production figure would be about 5 G.O$_2$/m.^{2}/day (ca. 2.5 G.C/m.^{2}/day) which is roughly equivalent to 18,206 kg./ha./yr. (16,243 lbs./acre/yr.) of dry organic material or an annual loss of about 25,841 metric tons (28,425 tons) for the 1,400 hectares (3,500 acres) of the bay now filled.

No quantitative study has been made of biomass of animals living among blades of turtle grass, although Moore (1963) and Stephens (1966) estimated the abundance of small invertebrates, and drop-net samples in Texas bays gave data on some larger invertebrates and fishes (Hellier, 1958, 1962; Jones, Ogletree, Thompson, and Klenniken, 1963). The drop-net studies gave a mean annual standing crop of about 15 g./m.^{2} wet weight (3 g./m.^{2} dry weight—20 percent of wet weight) (Vinogradov, 1953). Annual fish production is also about 3 g./m.^{2} in Texas bays or about 30 kg./ha./yr. (27 lbs./acre/yr.) (Hellier, 1962). This figure is below an estimate by Sykes (1963) for fishery production in Gulf estuaries (52 kg./ha./yr., or 46 lbs./acre/yr.). Using Sykes' estimate, we calculate that filling of 1,400 hectares (3,500 acres) has reduced fishery production in Boca Ciega Bay by 73 metric tons (80 tons) per year.

Biomass of invertebrate infauna living among roots and rhizomes of turtle grass was calculated from wet whole weight of animals recovered by sieving 0.25 m.^{2} plug samples collected in areas A, B, and C. At area D, the infauna biomass was determined in the same manner for unvegetated bottom (fig. 10). Mean wet weights of infauna in areas A, B, C, and D were 912, 560, 128, and 80 g./m.^{2}, respectively. Thus, the density of sea grass and abundance of infauna were positively correlated. If 85 percent of wet whole weight is weight of contained water and inert structures, dry weight of infauna from luxuriant beds of turtle grass in the lower bay was about 137 g./m.^{2} This figure is high in comparison with other biomass figures for estuarine waters (Sanders, Goudsmit, Mills, and Hampson, 1962). Bayfills in Boca Ceiga Bay have reduced the standing crop of bottom invertebrates by about 1,812 metric tons (1,993 tons)—calculated from relatively low infaunal biomass of area C.

Figures for the annual production of infauna are much higher. Sanders (1956) estimated infaunal production at two to five times the standing crop and indicated that the larger factor very likely applied in tropical situations. We arbitrarily selected four as a multiplier, and calculated infaunal production in the best stands of turtle grass at about 548 g./m.^{2}/yr. (5,466 kg./ha./yr., or 4,877 lbs./acre/yr. dry weight). Even in poor grass beds at area C infaunal production would be about 768 kg./ha./yr. or 685 lbs./acre/yr. This figure multiplied by the 1,400 hectares (3,500 acres) now in bayfills puts the loss of infaunal production at about 1,091 metric tons (1,200 tons/yr.). If more refined collecting had been done (screening at less than 0.701-mm. mesh), the addition of biomas from meiobenthos would have added considerably to the figures reported for macrobenthos alone, and the annual production of meiobenthos would very likely be equivalent or somewhat greater than the estimate for macrobenthos (Weiser, 1960; McIntyre, 1964).

ESTUARINE EVALUATION

Products and other values provided by the Nation's tidewaters are so numerous and diverse that their true worth is difficult to compute. Nonetheless, a number of attempts have been made to estimate the cash value of estuarine acreage. In the northeast, notable contributions were made by Shuster (1959); Fogg (1964); Jerome, Chesmore, Anderson, and Grice (1965); Jerome, Chesmore, and Anderson (1966); and Cain (1966). Pertinent details of estuarine evaluations along the Gulf of Mexico were abstracted and annotated by Woodburn (1965).

On the basis of these estimates, we conclude that fishery production alone in Tampa Bay estuary has an annual value of about $741/ha. ($300/acre). In addition, these waters are used by public utilities, industry, and commerce and serve recreational requirements of nearly a million residents[10] and 1½ million annual vacationers.[11] Hence, total worth of each water acre in the estuary can be conservatively estimated at $988/ha. ($400/acre) per year. At this rate, the 1,400 hectares (3,500 acres) covered by bayfills in Boca Ciega Bay represent an annual loss of about $1.40 million, which if capitalized at 6 percent would total a natural investment of $23.3 million. This accounting is not complete because the undesirable aspects of coastal development extend well beyond bulkheads and outfalls.

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[10] Tampa data, Greater Tampa Chamber of Commerce, Tampa, Fla.

[11] St. Petersburg Times, July 19, 1966.

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PHOTOGRAPHIC ATLAS OF SOCKEYE SALMON SCALES

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ABSTRACT

Photographic plates of sockeye salmon scales, with explanatory text, illustrate in detail the variations in scale features in this species. These illustrations of zones of fresh-water and ocean growth (and of complete scales) can be used as: (1) standards to which scales under study may be referred for determination of age and race, (2) guides in choosing scale characters for racial and other studies, and (3) aids in the training of scale scientists. Examples of regenerated, resorbed, and other atypical scales are also shown.

Sockeye salmon *(Oncorhynchus nerka)* is the most valuable species of Pacific salmon in North America and has been the subject of scientific study since the 1870's. Most of the extensive research for the INPFC (International North Pacific Fisheries Commission) by Canada, Japan, and the United States now is directed toward this species. Many of these projects use data obtained from study of the scales of sockeye salmon.

Sockeye salmon spend their early lives in fresh water, migrate to the North Pacific Ocean, and finally return to their natal streams to spawn and die. The growth zones formed on the scales record the growth of each individual fish. The fresh- and salt-water zones differ from each other in appearance. The zones can reveal the number of years that the fish spent in each environment; they also divulge the year in which the fish was hatched and the year it migrated to sea. Scale features have been used in age studies of sockeye salmon since 1910 (Gilbert, 1913). Recently, scale features have also been used in racial studies to determine the origin of fish taken at sea (Krogius, 1958; Kubo, 1958; Kubo and Kosaka, 1959; Henry, 1961; Mosher, Anas, and Liscom, 1961; Anas, 1963; Mosher, 1963; and Anas, 1964).

No detailed information has been published, however, on how to interpret the scales. The purpose of this atlas is to show the features of sockeye salmon scales in detail so that workers can interpret the scales they are working with to provide the data required in their studies.

A section on the use of the atlas in age studies and for describing scale features follows the illustrations of the scale features.

MATERIALS AND METHODS

Scientists of BCF (Bureau of Commercial Fisheries) have examined many thousands of sockeye salmon scales in recent years to supply information to the United States Section of INPFC. From these thousands I have selected certain scales to illustrate the variations in scale characters among fish. Variations may be genetic or environmental, or both, but generally many of the differences in the characters of scales are linked to geographic localities; therefore, a study of these variations offers a means of determining the mainland (racial) origin of fish taken beyond their natal streams.

For scale studies, workers of the research agencies of the INPFC (Fisheries Agency of Japan, Fisheries Research Board of Canada, and BCF) collect scales from the side of the fish as shown in Mosher, 1963. The "preferred scale" is in the second scale row above the lateral line in the diagonal scale row downward from the posterior edge of the dorsal fin. If this scale is missing on both sides of the fish, a scale is taken as close as possible to the preferred position, but not from the lateral line or the first row above or below the line.

The plates of the atlas are made from negative

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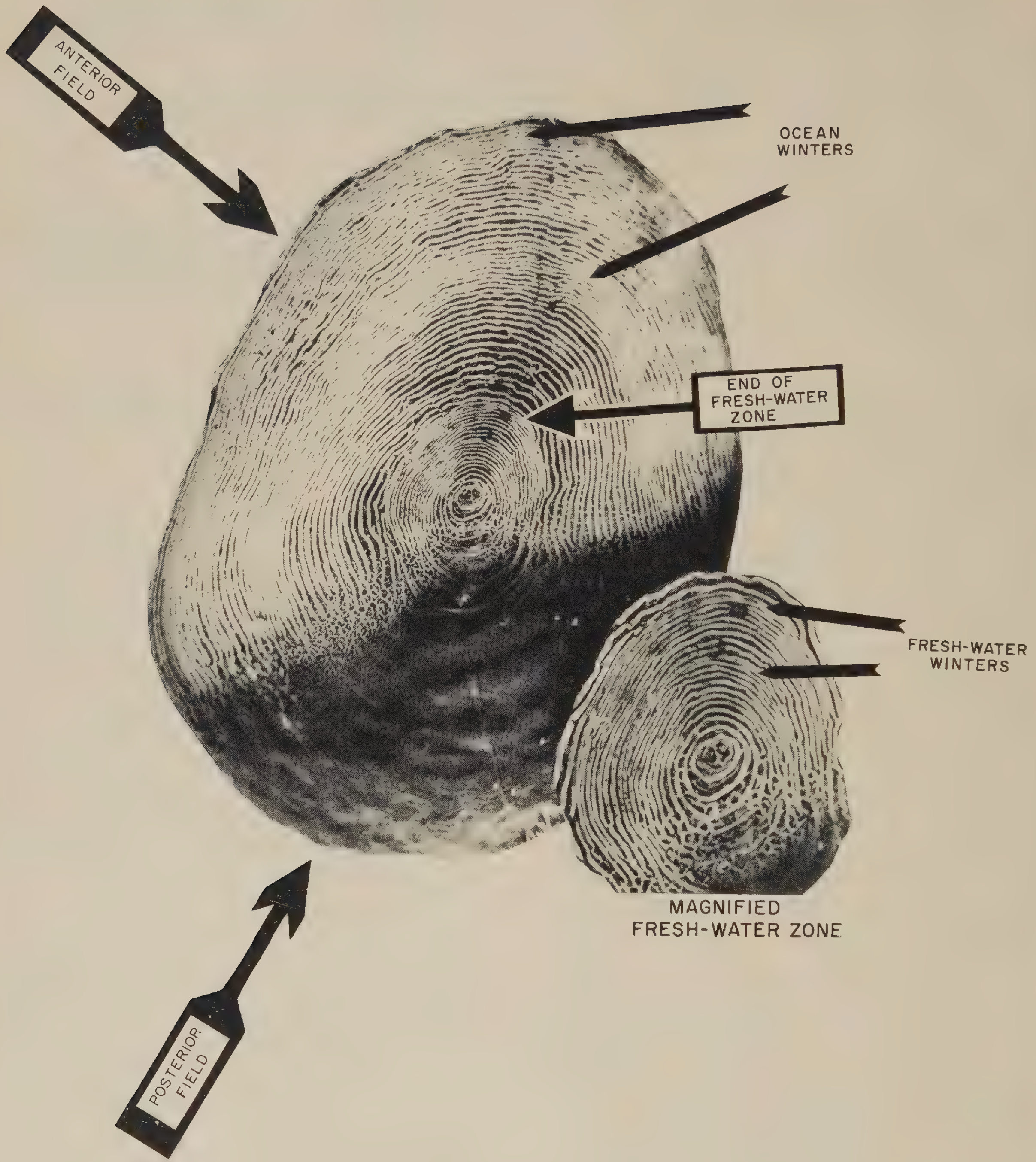
ANTERIOR FIELD
OCEAN WINTERS
END OF FRESH-WATER ZONE
FRESH-WATER WINTERS
MAGNIFIED FRESH-WATER ZONE
POSTERIOR FIELD

Plate 1.—Sockeye salmon scale.

prints of projected plastic impressions of scales.[1] Explanations and descriptions of the various features accompany the plates.

The original plates were assembled on 15- by 20-inch mounting sheets. Magnification of the individual scales and scale sections was adjusted for reduction onto the usual 8- by 10½-inch page; in this reduction, however, the clarity of the scale characters varies somewhat; therefore, I suggest that the reader keep a small magnifying glass (2 to 4X) handy for examination of specific portions of the plates as needed.

Examples of negative and positive prints of scales, a comparison of scales and their plastic impressions, the appearance of scale features under various magnifications, a glossary of terms used in scale studies, and the method of making the photographs are presented in the appendix.

The following order of topics has been chosen as the most useful for study of scales from sockeye salmon:

1. Gross features of sockeye salmon scales (plates 1 and 2).
2. Circuli, winter zones, and ages in the fresh-water growth zone (plates 3, 4, and 5).
3. Transition zone between fresh-water and ocean growth (plate 6).
4. Appearance, number, and spacing of circuli, winter zones, and ocean ages in the ocean growth zone (plates 7-11).
5. Age group combinations in sockeye salmon (plates 12-16).
6. Anomalies which make some scales unusable for age and racial studies (plates 17, 18, and 19).
7. Use of the atlas.
8. Appendix.

FEATURES OF SCALES FROM SOCKEYE SALMON (Plate 1)

Under magnification, a sockeye salmon scale shows two distinct areas: (1) The anterior or sculptured field, which was embedded in the scale pocket and (2) the posterior or unsculptured field, which protruded from the scale pocket and overlapped the adjacent posterior scale pockets. The examples shown in plate 1 and plate 2 illustrate these and other gross features described below. Scales of Pacific salmon are cycloid scales.

ANTERIOR FIELD

The upper surface of the anterior field is sculptured with ridges (circuli) and grooves (interspaces). See Koo and Finn (1964) for photographs of magnified cross sections of salmon scales. Under magnification the circuli and interspaces appear as alternating light and dark concentric "rings" which result from differences in transmission of light through the grooves and ridges of the translucent scale material.[2] The contrast between circuli and interspaces varies from high (heavily marked circuli) to low (lightly marked circuli).[3] Circuli are formed on the edge of the scale as it grows (Neave, 1936; Welander, 1940; Wallin, 1957). When the scales are growing rapidly (in late spring and summer), the circuli are deposited relatively far apart and have a broad and heavy appearance and texture (as if drawn with a blunt pencil or stub-tipped pen). The periods of retarded growth (in the fall, winter, and early spring) show on the scale as bands of circuli lying closer together than the circuli of the summer growth zone. These bands have been called annual marks, annual rings, winter zones, winter checks, winter growth zones, resting zones, or annuli.[4] Where zone dimensions are needed, most salmon scale workers measure to the last circulus of this band of closely spaced circuli.

The circuli laid down while the fish is in fresh water are of finer texture than those deposited later while the fish is in the ocean (as if drawn with a sharp pencil or fine-tipped pen). This cen-

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[1] See Mosher (1950) for a description of the scale projector. See Clutter and Whitesel (1956) or Koo (1962a) for a description of the method of making plastic impressions of the scales.

[2] The circuli appear as the light rings in the negative prints and the interspaces as the dark rings (see appendix plate 3).

[3] The differences in contrast between circuli and interspaces are not as evident in the photographs as they are when the scales or scale impressions are examined directly. For reproduction I have adjusted the contrast between the light and dark tones to near maximum wherever possible.

[4] Annuli of sockeye salmon scales, unlike those of most other fish, are bands of closely spaced circuli formed during the winter and early spring. The usual definition of an annulus as a line of discontinuity between successive growth zones does not describe most annuli in the ocean growth zones of the sockeye salmon scale. Such lines of discontinuity often occur between the fresh-water and ocean growth zones whether or not an annulus is present and often occur on the scale at various places not related to the presence of the bands of closely spaced circuli which form each winter.

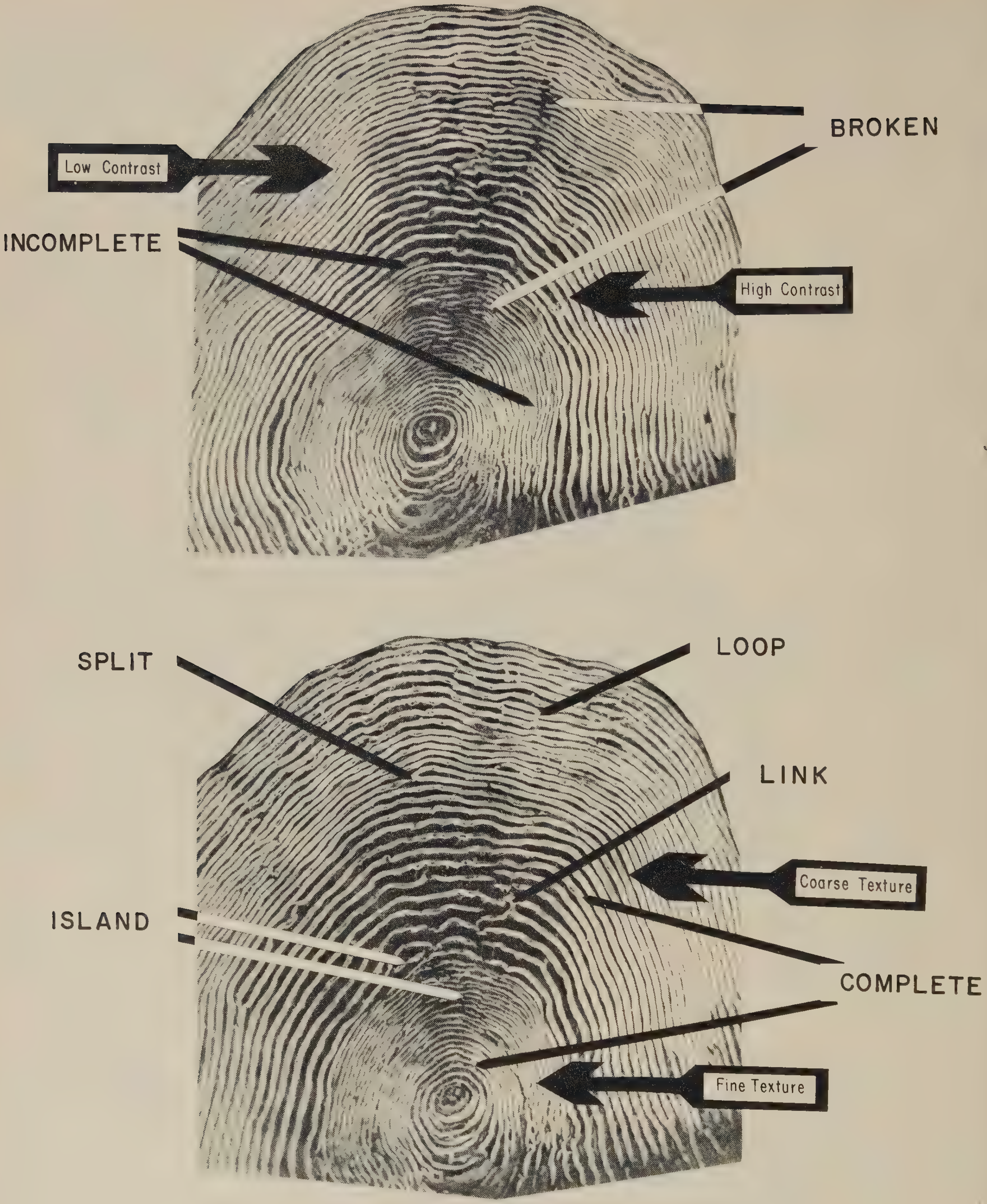
BROKEN
Low Contrast
INCOMPLETE
High Contrast
SPLIT
LOOP
LINK
Coarse Texture
ISLAND
COMPLETE
Fine Texture

PLATE 2.—Types of circuli.

tral zone of closely spaced circuli is often called the nucleus. The area enclosed by the first circulus is called the focus of the scale or the central platelet. Only the first few circuli encircle the focus; the rest are arcs that do not extend into the posterior field.

POSTERIOR FIELD

The posterior field is a relatively clear area without distinctive growth features. It photographs black because it is uniformly translucent (see appendix plate 3).

TYPES OF CIRCULI (Plate 2)

The circuli of fresh-water and ocean growth may be described as:

1. Complete, or regular—circuli that are unbroken over most of their arc.
2. Incomplete, or irregular—circuli that are broken, split, or otherwise discontinuous in the anterior portion of their arc. Several types of incomplete or irregular circuli may be identified as follows:
   - a. Broken—circuli that are broken or discontinuous in the anterior portion of their arc.[5]
   - b. Split—circuli that divide into two or more circuli.
   - c. Incomplete—circuli that end in a cul-de-sac against another one or two circuli, or circuli that are not complete around the anterior field of the scale.
   - d. Island—a small segment of a circulus that is not joined to another circulus, but stands by itself.
   - e. Loop—a segment of one or two circuli that form a loop.
   - f. Link—an interconnection between adjacent circuli.
   - g. Miscellaneous—circuli that are modified in various other ways.

FRESH-WATER (LACUSTRINE) GROWTH

Plates 3, 4, and 5 show the fresh-water portions of adult sockeye salmon scales and give examples of zones of complete, "average," and irregular circuli; various types of winter zones; and various fresh-water ages. The same criteria can be applied to scales from young salmon collected in fresh water.

FRESH-WATER CIRCULI (Plate 3)

This plate shows examples of different types of circuli in fresh-water growth of ages 1., 2., and 3.[6] See plate 2 for examples of various types of circuli. Figures labeled A are scales with predominantly complete circuli; those labeled B are more or less "average" scales, some circuli complete, others broken and irregular; and those labeled C are scales with predominantly broken and irregular circuli. Arrows indicate end of winter growth.

On the North American side of the Pacific Ocean complete circuli generally predominate on scales of fish from Bristol Bay, Karluk River, Fish Creek (in Cook Inlet), Alaska; Skeena and Fraser Rivers, British Columbia; and the Columbia River. On the Asian side of the Pacific, complete circuli occur frequently on scales of fish from the Ozernaia, Kamchatka, and Dalinaia Rivers of Kamchatka.

Broken and irregular circuli predominate on scales of fish collected in the Aleutian Islands, the Alaska Peninsula, Cook Inlet (except Fish Creek), and Southeastern Alaska; Smith and Rivers Inlets, British Columbia; and in Blinjinaia and Bolshaia Rivers of Kamchatka.

Fish scales from any area may have some complete and some broken circuli in the fresh-water zones.

WINTER ZONES IN FRESH-WATER GROWTH (Plate 4)

As mentioned previously, winter zones are formed when the growth of the scale slows down during the fall, winter, and early spring. The circuli are formed closer together and are broken or otherwise interrupted so that the winter growth zone shows up as a band of circuli more closely spaced than the adjacent circuli nearer

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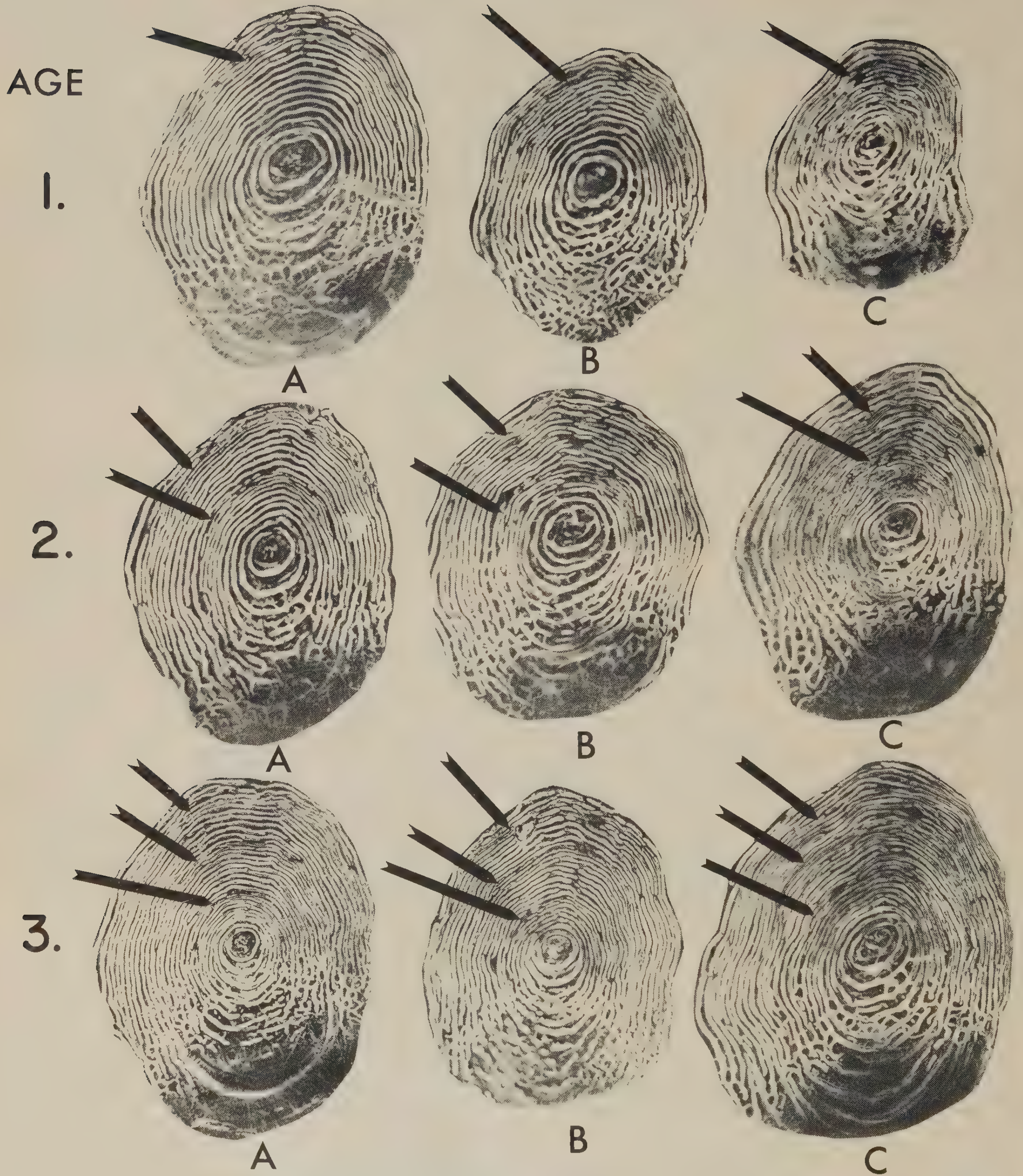
[5] Krogius (1958) used counts of broken circuli as a scale character in racial studies.

[6] Age designation of salmon in reference to fresh-water life only follows the recommendations of Koo (1962b): an Arabic numeral indicating the winters the fish spent in fresh water from hatching, followed by a dot.


AGE
1.
2.
3.
A
B
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A
B
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A
B
C

Plate 3.—Fresh-water circuli.

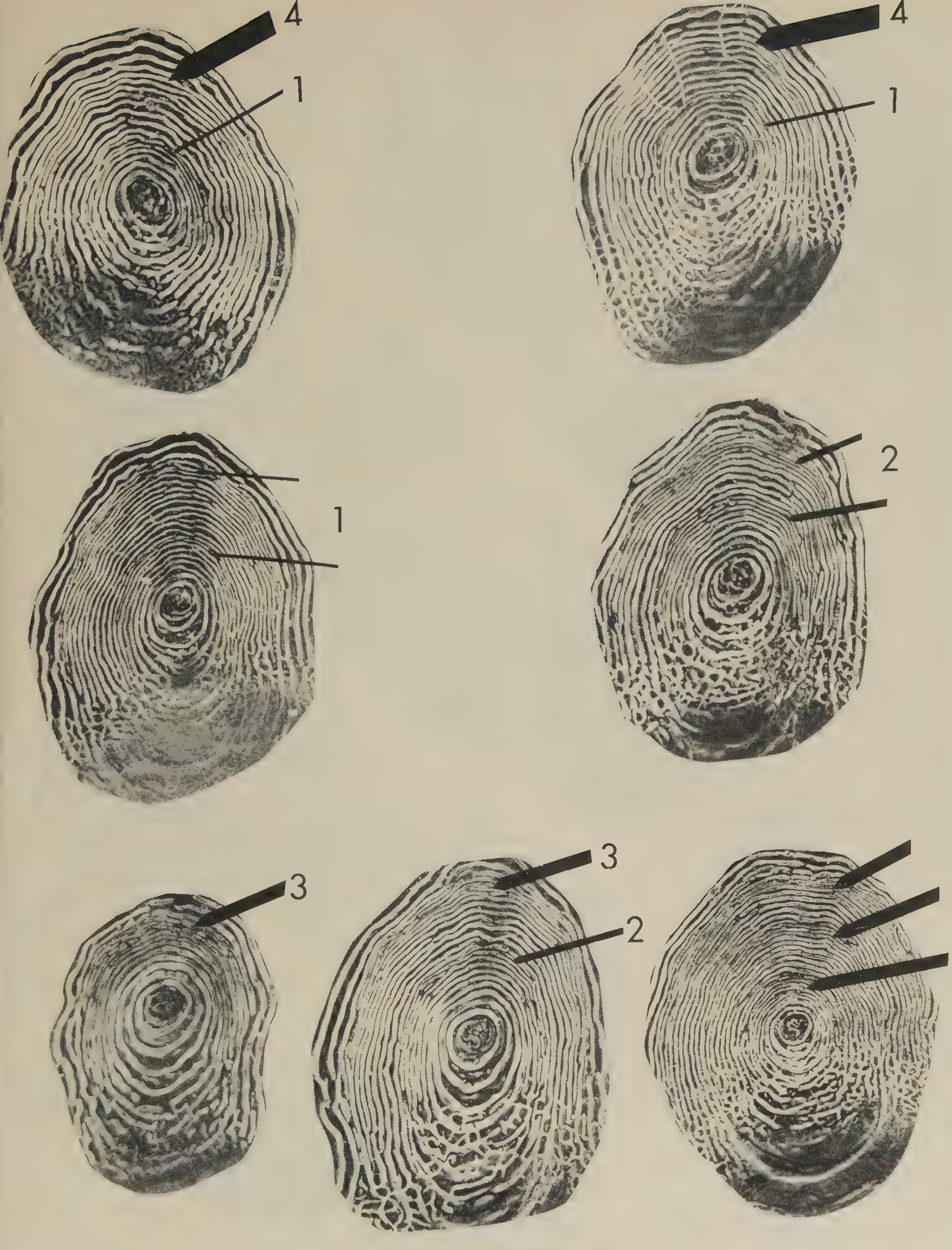
4
1
4
1
1
2
3
3
2
3

PLATE 4.—Winter zones in fresh-water growth.

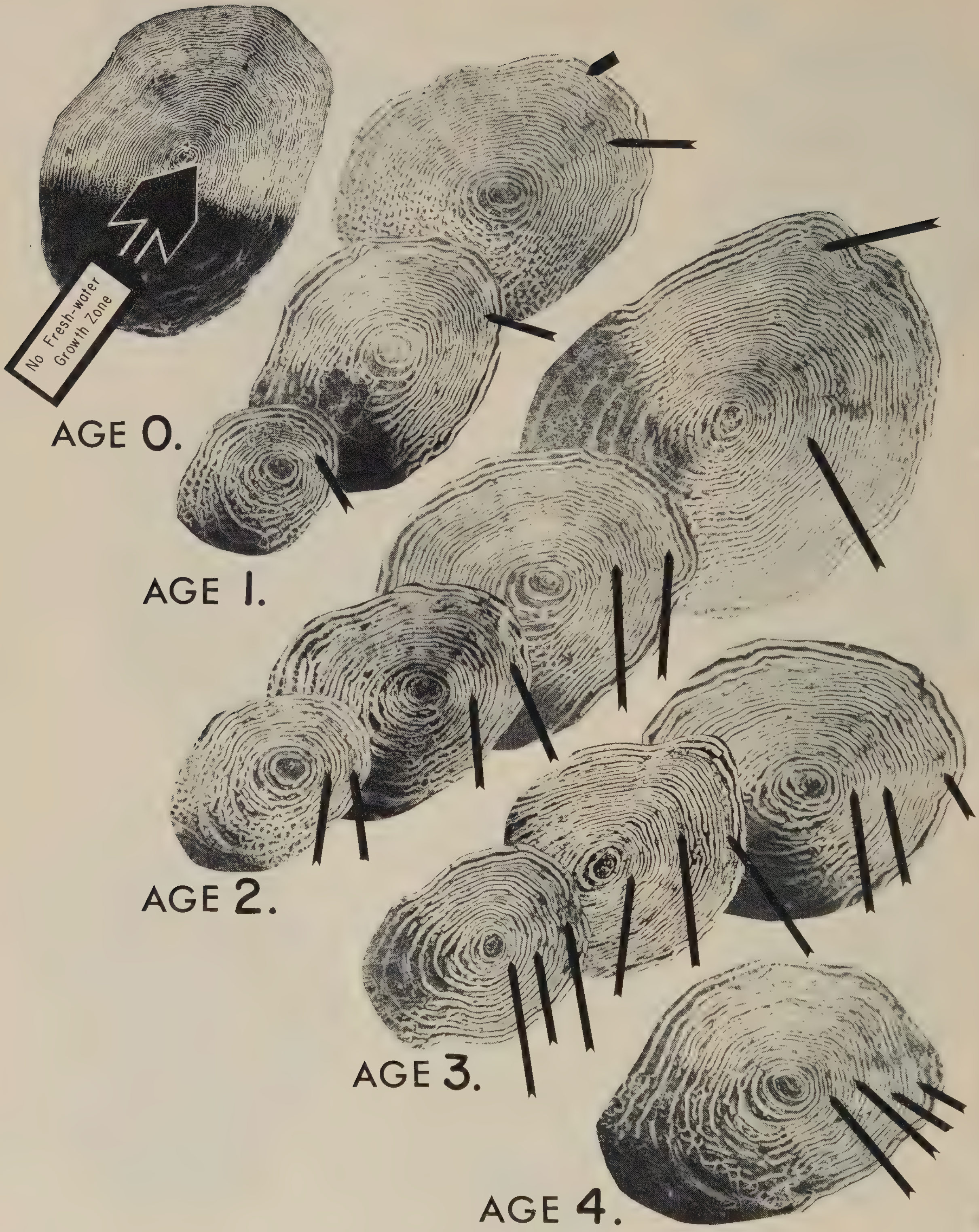
No Fresh-water Growth Zone
AGE 0.
AGE 1.
AGE 2.
AGE 3.
AGE 4.

PLATE 5.—Fresh-water ages.

to the focus or to the edge of the scale. Because the circuli of the fresh-water zone are closer together and more finely lined and the growth zones may be composed of fewer circuli than in the ocean, the winters of fresh-water growth are sometimes indistinct and difficult to identify.

To assist in interpretation of the fresh-water zone, winter growth zones are classified into four types (numbers 1 to 4 in plate 4 correspond with the following descriptions):

1. Those made up of two or three circuli close together. This type of winter zone is the most distinct and easiest to identify and measure because it looks almost like a continuous line around the anterior field. The width of the arrows indicates the relative width of the winter zone.
2. Those made up of three or more circuli lying close together in a narrow band. This type of zone is relatively easy to identify, but less easy to measure or delimit than those of type 1.
3. Those made up of a number of complete or broken circuli lying close together in a broader band than those of type 2.
4. Those made up of a few circuli that are not much closer together than the adjacent circuli of the summer growth. These zones are diffuse and difficult to identify and measure.

FRESH-WATER AGES (Plate 5)

Plate 5 shows the range of fresh-water ages and the range of sizes of fresh-water zones of each age that may be found in sockeye salmon scales. The complete scale of the O. age fish is magnified about 20 X. All other photographs are of the fresh-water zones of scales from adult sockeye salmon and show the relative sizes of the various zones as they appear when projected at about 40 X. The winters in fresh water are indicated by arrows.

Age 0. A complete scale from a fish in its third year that migrated to the ocean soon after hatching, magnified about 20 X. The few sockeye salmon that migrate seaward early in their first year usually reach the ocean before scales are formed; thus, their scales lack a fresh-water growth zone. Additional examples are shown in plate 12 and in Koo (1962c).

Age 1. Scales from fish that migrated seaward after one growing season in fresh water (in the second year). Small to large zones are illustrated. The small zone is typical of fish from Southeastern Alaska and some British Columbia areas. The large zone is typical of fish from Fish Creek, Cook Inlet, Alaska. (The stub pointer near the top of the upper scale in this series indicates the end of the transition zone; see plate 6.)

Age 2. Scales from fish that migrated to the sea after two full growing seasons in fresh water (in their third year). Small to very large zones are shown. The small zone is common in fish from Asian areas. The very large ones have been found only in fish from Dalinaia River, Kamchatka.

Age 3. Scales from fish that migrated to the sea after three full growing seasons in fresh water (in their fourth year). Small to large zones illustrated. The small zone is common in fish from Asian areas.

Age 4. A scale from a fish that migrated to sea after four full growing seasons in fresh water (in its fifth year). Fish of this fresh-water age are rare.

TRANSITION ZONE BETWEEN FRESH-WATER AND OCEAN GROWTH (Plate 6)

Correct interpretation of the zone of transition between fresh-water and ocean growth is important in age determination. Many disagreements on the age of individual sockeye salmon can be traced directly to different interpretations of this portion of the scales.

In most areas of western Alaska, new growth beyond the zone of narrow winter circuli is evident on the margin of nearly all scales of young fish in fresh water by mid-June (Koo, 1962a; and Mosher[7]) and earlier in areas to the south.

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[7] Mosher, Kenneth H. Time of fresh-water annulus formation on the scales of young sockeye salmon from western Alaska. U.S. Fish and Wildlife Service, Bureau of Commercial Fisheries Biological Laboratory, Seattle, Wash. [Manuscript.]

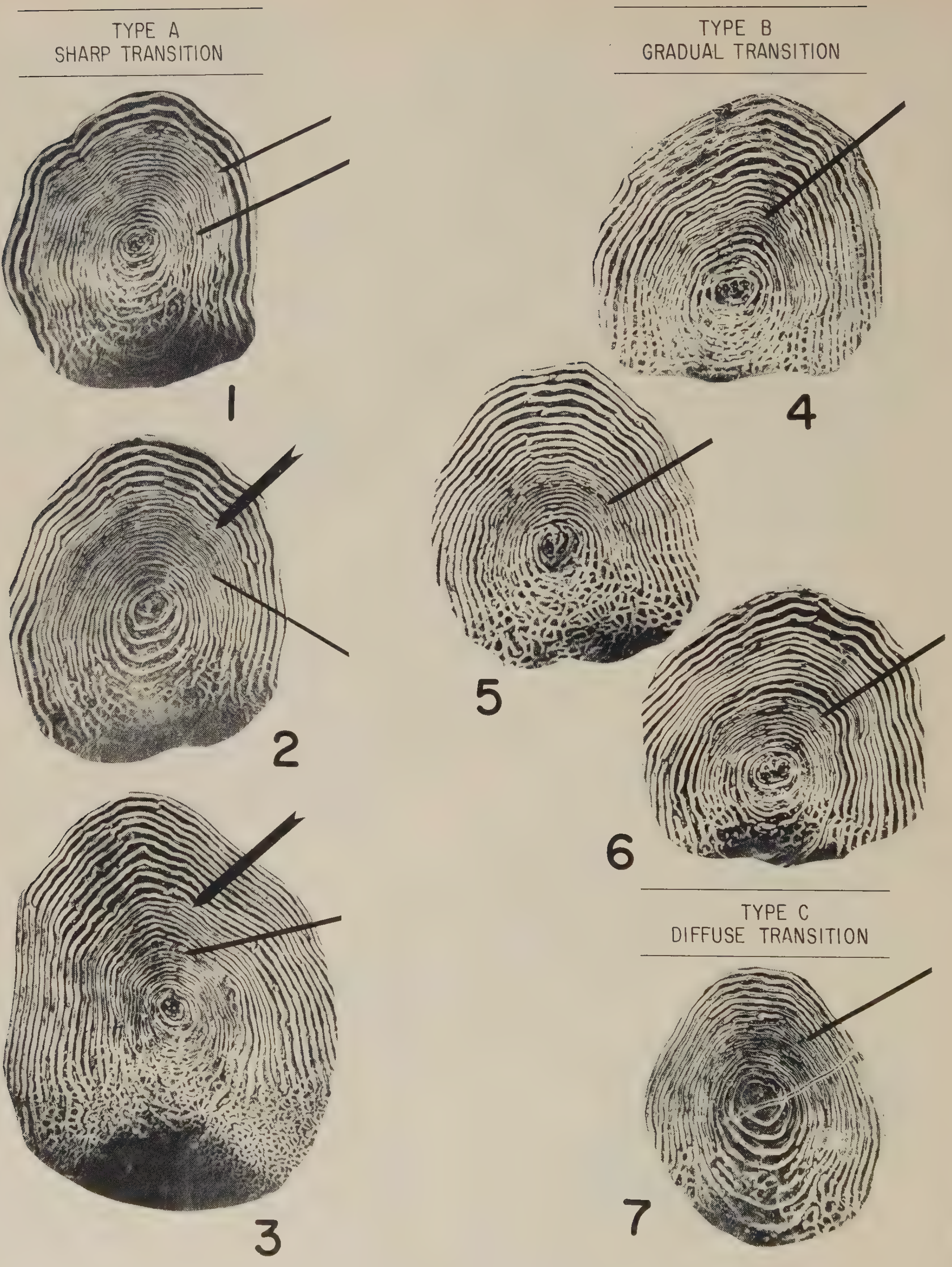
TYPE A
SHARP TRANSITION
TYPE B
GRADUAL TRANSITION
1
4
5
2
6
TYPE C
DIFFUSE TRANSITION
3
7

PLATE 6.—Transition zone between fresh-water and ocean growth.

Wider, darker circuli usually are laid down after this zone in the year in which the fish migrates seaward. If the fish reaches the ocean about the time this zone of narrow circuli is completed, the transition from narrow, light-textured fresh-water circuli to wider, heavier textured ocean circuli is abrupt. If the winter zone is completed before the fish reaches salt water, however, a varying number of circuli, intermediate in appearance between the fresh-water and ocean circuli, may be formed. This type of growth is called plus, transitional, intermediate, incidental, or spring growth.[8]

If the transition zone merges gradually into the ocean growth zone, it is usually easy to identify, although not to delimit. If, on the other hand, an adventitious mark (called a "migration check") forms and the zone is large, the migration check might be mistaken for another fresh-water winter (Mosher[9]).

Three general types of transition between fresh-water and ocean growth zones can be identified: type A, sharp or abrupt; type B, gradual; and type C, diffuse. These general types can be found in fish of all fresh-water ages.

Examples of the three types of transition zones are shown in plate 6. (The winter zones are indicated by arrows, and the migration checks in figures 2 and 3 by wider arrows.)

Type A. Sharp or abrupt transition is shown by the following photographs:

Figure 1. No plus growth. The transition from the fine-lined, closely spaced fresh-water circuli to the widely spaced ocean circuli is sudden. This type of transition poses no problems for accurate age determination.

Figure 2. Little plus growth after the winter zone formed. A migration check is between the transitional growth and the ocean growth. That the portion of the scale between the two arrows is plus growth is evident from the narrowness of the zone and the appearance of the circuli, which are intermediate in width and spacing between the circuli of the fresh-water and ocean growth zones.

Figure 3. Extensive plus growth after the winter zone formed. The weak migration check at the end of the transition might be mistaken for another winter in fresh water. Note, however, that the seven or eight circuli immediately preceding the broad, widely spaced circuli of the ocean zone are intermediate in width and spacing between the circuli of the fresh-water and ocean growth zones.

Type B. Gradual transition is shown by the following photographs:

Figure 4. No plus growth. The two or three circuli following the winter zone gradually expand into the broader ocean-type circuli.

Figure 5. Little plus growth. A few circuli of intermediate type are present, and the boundary of the transition is difficult to identify.

Figure 6. Extensive plus growth. The zone of intermediate growth is wide. Because there is no migration check at the end of the plus growth, the chance is small that it will be interpreted as another year's growth in fresh water.

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[8] The term "spring growth" is usually applied to the intermediate or plus growth observed on scales of seaward migrant fish, not adult fish.

[9] Mosher, Kenneth H. The plus or intermediate growth of sockeye salmon scales. Bureau of Commercial Fisheries, Biological Laboratory, Seattle, Wash. [Manuscript.]

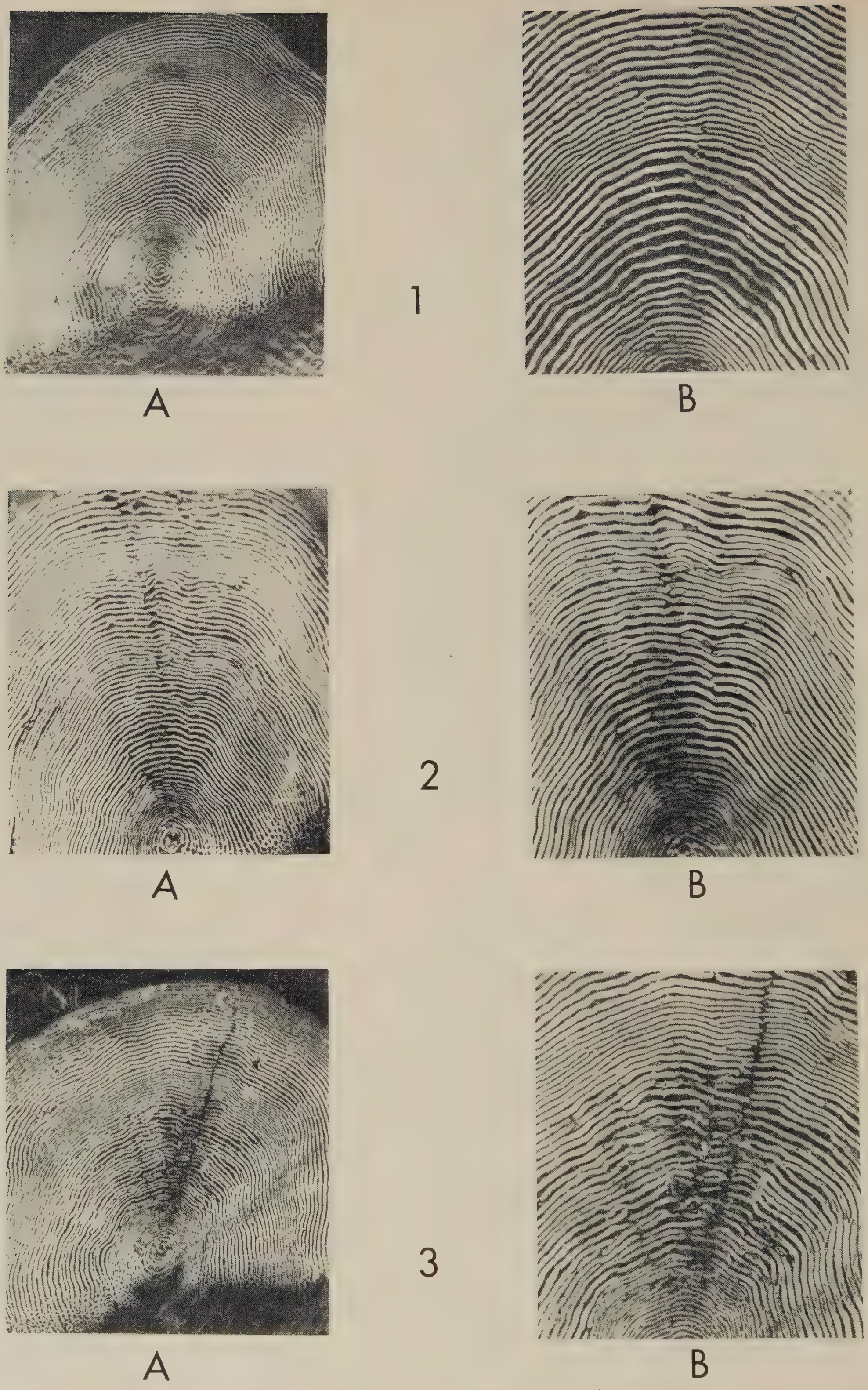


PLATE 7.—Appearance of ocean growth zones based on type of circuli.

Type C. Diffuse transition is shown in figure 7. The transition between the fresh-water and ocean growth is so broken up by irregular circuli that the exact boundaries of the fresh-water and plus growth (if any) are difficult to determine.

OCEAN GROWTH

The following plates show details of the ocean growth zone, including the variations in:

1. appearance of zones based on type of circuli (plate 7).
2. number of circuli (plate 8).
3. spacing of circuli within the zones (plate 9).
4. appearance of the winter zones (plate 10).
5. ocean ages (plate 11).

APPEARANCE OF OCEAN GROWTH ZONES BASED ON TYPE OF CIRCULI (Plate 7)

The relative numbers of complete and interrupted circuli affect the appearance of the different ocean zones and the ease and accuracy with which measurements and counts of circuli and winters of life can be made. See plate 2 for examples of various types of circuli. Three broad categories of ocean growth zones, based on the circuli, are illustrated in plate 7. Each category is illustrated by two photographs.

Figure A shows the major portion of a scale magnified about 20 X; figure B, which is the central portion of the same scale magnified about 40 X, shows the circuli of the first ocean zone in greater detail. The categories of ocean-growth zones are described as follows:

Category 1. A scale with mostly complete circuli in the ocean-growth zones.

Category 2. A scale with complete and irregular circuli in the ocean-growth zones (an "average" scale).

Category 3. A scale with nearly every circulus broken or otherwise interrupted in the ocean-growth zones.

NUMBER OF OCEAN CIRCULI (Plate 8)

The mean number of circuli in the first ocean growth zone of scales from adult fish differ by geographical areas (table 1). The largest mean numbers are on scales of sockeye salmon from Rivers Inlet, British Columbia. Mean numbers of circuli tend to be progressively lower on scales of North American fish taken southward to the Columbia River and northwestward to Bristol Bay, Alaska. Scales from Asian fish have greater mean numbers of circuli than the Bristol Bay sockeye. This difference in mean numbers of circuli holds true in all ocean zones but is most pronounced in the first ocean zone.

The scales in plate 8 were selected to show the numerical differences in the number of circuli in the first ocean zone (number of circuli between each pair of pointers) among sockeye salmon from different geographical areas, as follows:

Figure 1. Asia, 25 circuli.

Figure 2. Bristol Bay, 22 circuli.

Figure 3. Ketchikan, Alaska (as representative of the area from Cook Inlet to the Nass River, British Columbia), 27 circuli.

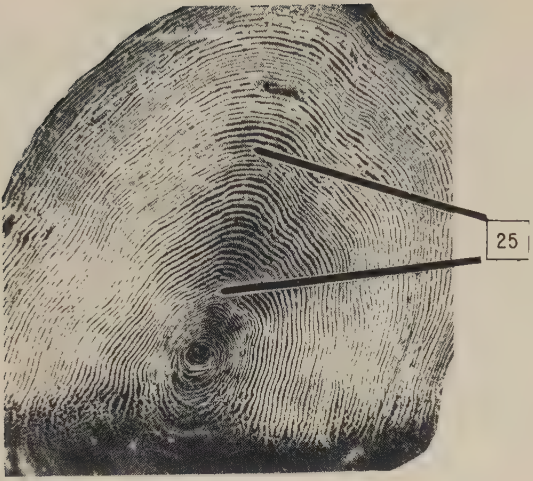
Figure 4. The Skeena River, British Columbia, 29 circuli.

Figure 5. Rivers Inlet, British Columbia, 32 circuli.

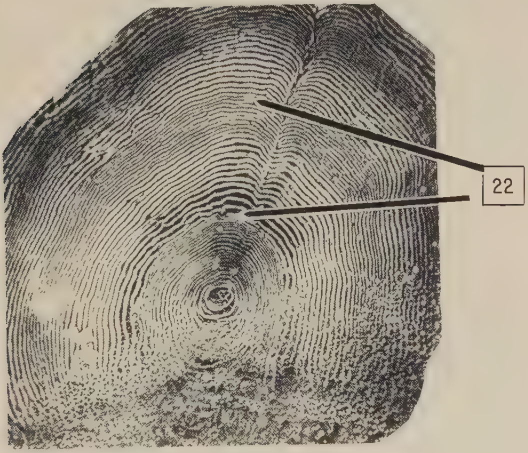
Figure 6. The Columbia River, Oregon-Washington, 26 circuli.

SPACING OF OCEAN CIRCULI (Plate 9)

Spacing of circuli within the ocean growth zones may also vary between scales from fish collected in different geographical areas. In general, scales with relatively large numbers of circuli in the first ocean zone tend to have more uniformly spaced circuli than those with fewer circuli. On scales from Bristol Bay fish, the widest spaced circuli are usually deposited near the closely spaced fresh-water portion. On scales from Asian fish, the widest spaced circuli are often deposited just before the closely spaced winter ocean circuli. On scales from fish taken east and southeastward of Bristol Bay, the position of the widest spaced circuli of the ocean zones is less consistent. They may occur in the same position as in the Bristol Bay or the Asian



1



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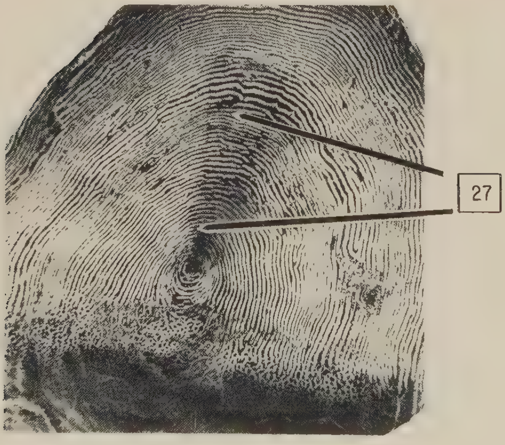

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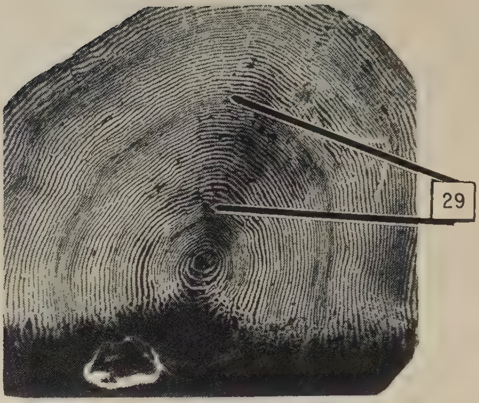

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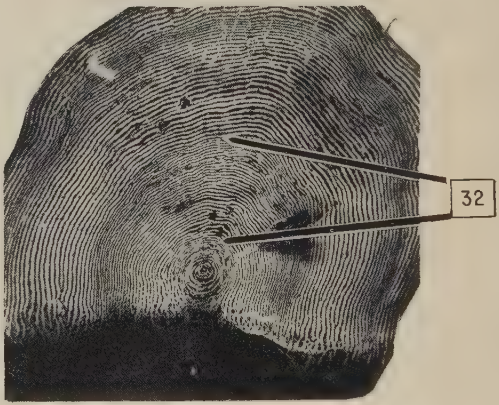

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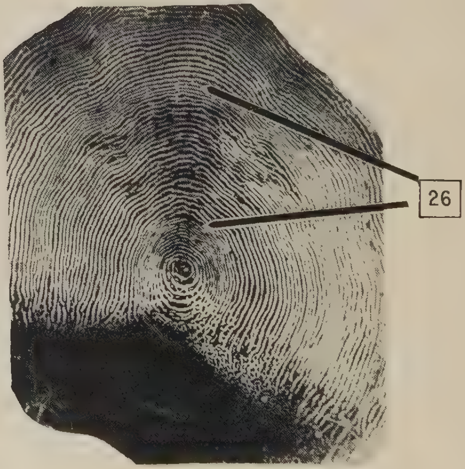

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PLATE 8.—Number of ocean circuli.

TABLE 1.—*Percentage frequency distribution*[1] *and mean number of circuli in the first ocean zone of scales from sockeye salmon collected in 1963*

[Asterisks indicate modes]

Number of circuli	Asia[2]	Alaska			British Columbia				Columbia River[3]
		Bristol Bay[2]	Chignik[3]	Cook Inlet[2]	Nass[2]	Skeena[3]	Rivers Inlet[3]	Fraser[3]	
	Percent								
13	0.2	----	----	----	----	----	----	----	----
14	.5	----	----	----	----	----	----	----	----
15	.2	0.5	----	----	----	----	----	----	----
16	----	1.5	----	----	----	----	----	----	----
17	.5	4.4	----	----	----	----	----	----	----
18	1.4	9.1	0.6	----	----	----	----	----	----
19	3.1	14.7	1.4	0.4	0.6	----	----	----	----
20	6.5	*19.1	2.3	2.0	1.5	----	----	----	----
21	9.0	18.7	4.5	4.6	2.0	----	----	----	0.9
22	9.3	14.5	8.5	7.3	1.8	0.6	----	----	4.0
23	11.9	10.0	14.2	10.4	2.6	1.7	----	0.3	7.3
24	*15.9	5.2	*17.3	14.6	5.6	4.8	----	3.4	9.8
25	15.4	1.7	15.6	*17.8	9.2	10.5	0.3	9.2	14.0
26	10.6	.5	13.4	16.0	13.0	15.1	.9	12.9	*18.0
27	5.9	.1	9.9	12.1	*14.4	*15.6	1.2	*14.7	16.8
28	3.8	----	6.0	7.9	12.2	13.6	2.9	*14.7	12.2
29	2.5	----	3.7	3.7	10.2	12.2	6.2	13.6	8.2
30	1.4	----	2.0	2.1	10.2	10.2	8.8	11.5	5.2
31	1.0	----	.6	1.1	9.0	6.8	12.0	6.9	2.4
32	.7	----	----	----	5.4	4.0	*14.7	4.3	.9
33	.2	----	----	----	1.7	2.3	*14.7	4.3	.3
34	----	----	----	----	.4	1.1	11.5	2.8	----
35	----	----	----	----	.2	.6	7.9	1.1	----
36	----	----	----	----	----	.6	7.4	.3	----
37	----	----	----	----	----	.3	6.2	----	----
38	----	----	----	----	----	----	3.5	----	----
39	----	----	----	----	----	----	1.5	----	----
40	----	----	----	----	----	----	.3	----	----
Mean number of circuli	24.1	20.6	24.7	25.1	27.5	27.9	32.8	28.4	26.3
Number of fish	156	650	88	145	98	88	85	87	82

[1] Actual frequencies smoothed according to Henry (1961).

[2] Combined 1. and 2. fresh-water ages.

[3] 1. fresh-water ages only.

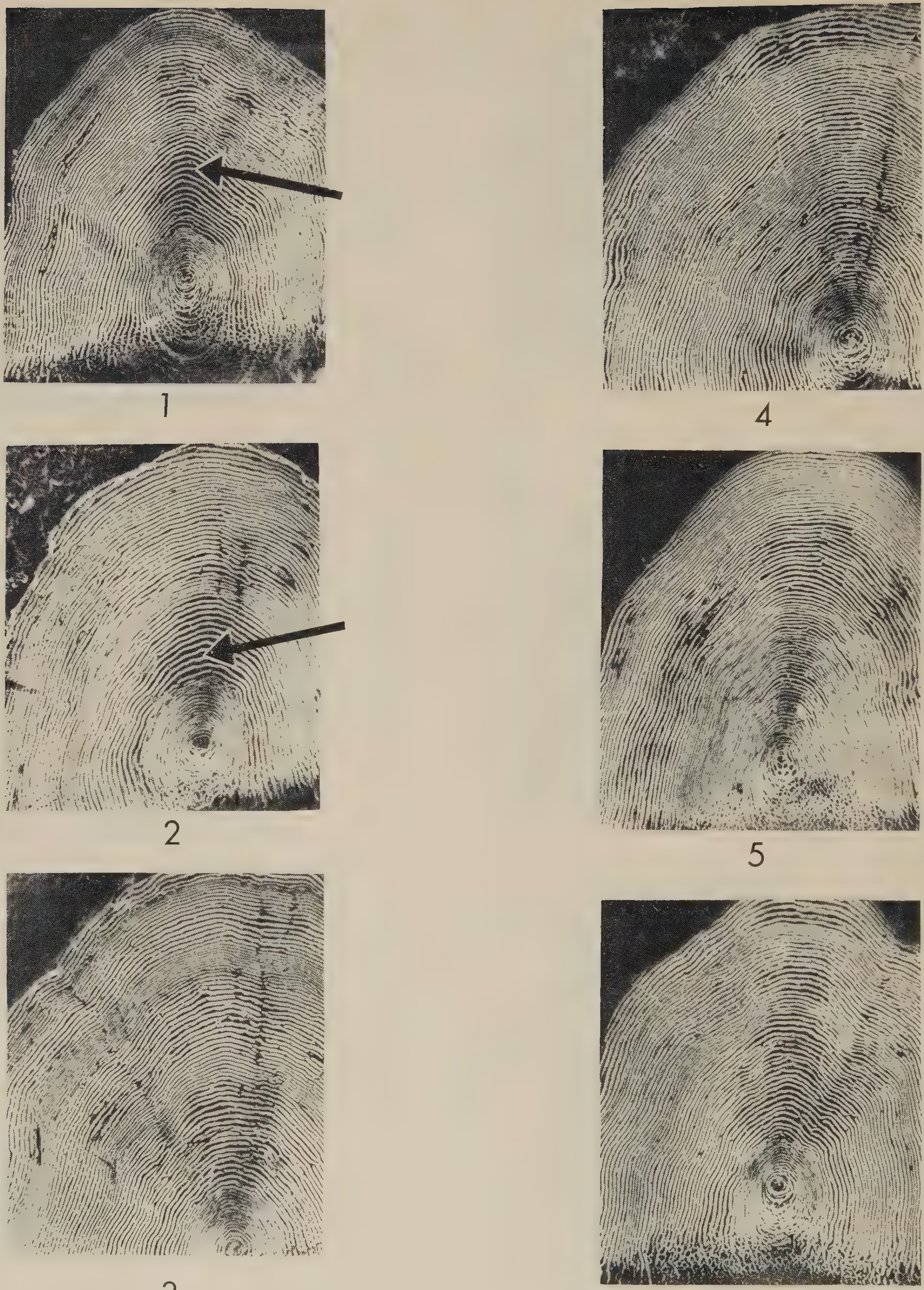

PLATE 9.—Spacing of ocean circuli.

fish, but often the circuli are so uniformly spaced that no area of widest spacing can be identified.

Plate 9 shows examples of these variations in spacing of circuli within the first ocean growth zone, as follows:

Figure 1. A scale from an Asian sockeye salmon with the widest spaced circuli (arrow) immediately preceding the winter ocean growth.

Figure 2. A scale from a Bristol Bay sockeye salmon with the widest spaced circuli (arrow) formed immediately after migration to the ocean.

Figure 3. A scale from a Cook Inlet sockeye salmon with a summer growth zone of widely and uniformly spaced circuli.

Figure 4. A scale from a Skeena River sockeye salmon with a summer growth zone of uniformly spaced circuli.

Figure 5. A scale from a Rivers Inlet sockeye salmon with a summer growth zone of evenly and closely spaced circuli.

Figure 6. A scale from a Columbia River sockeye salmon with a summer growth zone of widely and uniformly spaced circuli.

WINTER ZONES IN OCEAN GROWTH (Plate 10)

Winter zones in the ocean growth result from slower scale growth in the fall, winter, and early spring, during which time the circuli are formed closer together than during the faster growth in the late spring and summer. Zones of winter growth in the ocean, like those in the fresh-water portion of the scale, also vary in appearance; they may be classified into four general groups on the basis of appearance (winter zones in the illustrations are numbered as follows):

1. Clear-cut zones made up of a number of closely spaced circuli.
2. Zones made up of circuli less closely spaced or more numerous than those of group 1.
3. Diffuse zones the boundaries of which cannot easily be identified. Whereas the circuli are closer together than the adjacent summer growth zones, either the difference between the spacing of circuli is so slight or the narrowing of the circuli into the winter zone is so gradual that it is difficult to be sure of the exact boundaries of the zone.
4. Winter zones characteristic of the first ocean zone of most sockeye salmon from Rivers and Smith Inlets, British Columbia, where the circuli are often only slightly closer together than the closely spaced circuli of the summer growth.

The winters of ocean life of the fish not only must be accurately identified for age determination, but their location and boundaries must be measured exactly in many racial and other studies; therefore, scales with diffuse winter zones (group 3) may be difficult or impossible to use in some of these studies.

AGE GROUPS BY NUMBER OF WINTERS IN THE OCEAN (Plate 11)

Sections of sockeye salmon scales showing ocean growth zones illustrate the range of ocean ages found in this species.[10] Arrows indicate the winter growth zones.

.0 — only a few months in the ocean, no winter growth zone
.1 — one winter in the ocean
.2 — two winters in the ocean
.3 — three winters in the ocean
.4 — four winters in the ocean
.5 — five winters in the ocean

SCALES WITH DIFFERENT COMBINATIONS OF FRESH-WATER AND OCEAN AGE

All the combinations of fresh-water and ocean age that I have found in sockeye salmon are illustrated in plates 12 to 16. Age designations of adult salmon follow the recommendations of Koo (1962b). Two methods may be used—the European method or the Gilbert and Rich (1927) method. The Gilbert and Rich method is used on the following plates; in the text, age designa-

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[10] Age designation of salmon in reference to marine life only follows the recommendations of Koo (1962b): a dot followed by the number of winters the fish spent in the ocean.

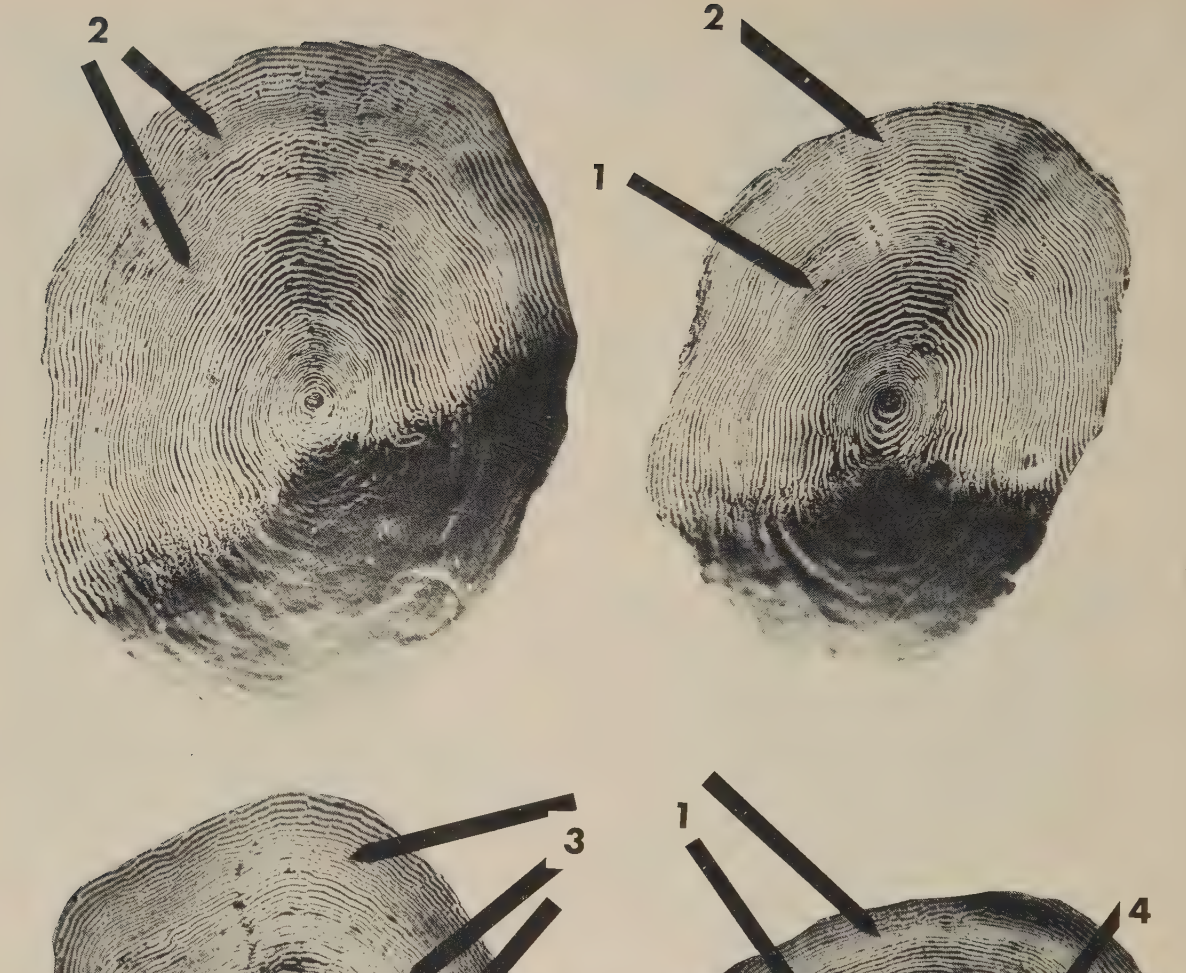

PLATE 10.—Winter zones in ocean growth.

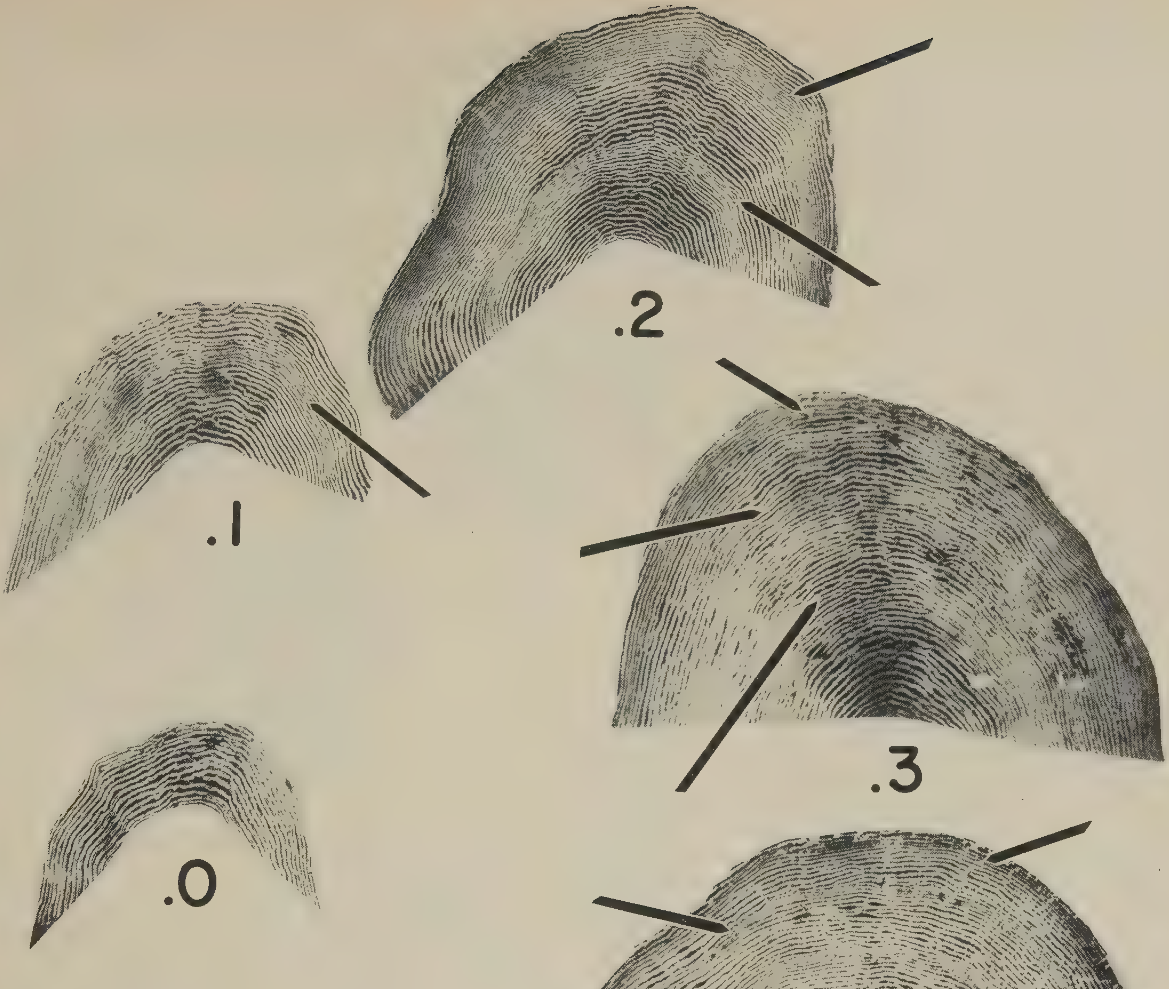

PLATE 11.—Age groups by number of winters in the ocean.

tion by the European method is shown in parentheses.

In the Gilbert and Rich designations, an Arabic numeral indicates the number of winters from spawning of the parents to capture. A second digit, usually written as a subscript, indicates the winters from spawning of the parents to seaward migration. Because the fish do not form scales until after the first winter in the gravel, the number of winters of growth is one less than shown by the age formula, but the fish is in the indicated year of life. To assign a fish to its parent brood year, subtract the first digit from the year of capture; e.g., a fish of age group 5_3 caught in 1965 was produced by the spawning in 1960 and migrated to the ocean in 1963. Scientists of the U.S.S.R. use a modified Gilbert and Rich system in which the age is computed from hatching instead of spawning of the parents (Krogius, 1958; Chugunova, 1959).

In the European method, the number of winters the fish spent in fresh water from hatching and in the ocean are separated by a dot. To determine the year of spawning that produced the fish, add 1 to the sum of the two digits and subtract from the year of capture.

A comparison of the major age groups in the three methods of age designation follows:

Gilbert and Rich	European	U.S.S.R.
4_1	0.3	3_0
4_2	1.2	3_1
5_2	1.3	4_1
5_3	2.2	4_2
6_3	2.3	5_2
6_4	3.2	5_3
7_4	3.3	6_3

Runs of sockeye salmon often include individuals, considerably smaller than the average, that have returned to spawn after only one winter at sea. These fish are known as "jacks" as they are almost invariably males, except in the Columbia River where they may be of either sex.[11]

In the following plates the winter growth zones are indicated by arrows—wide arrows in the ocean portion of the scale (plates 12-18) and narrow arrows in the fresh-water portion (plates 13-18). Stub arrows when present indicate the end of plus growth.

AGE GROUPS WITH NO SCALE GROWTH IN FRESH WATER (Plate 12)

Fish of these age groups migrate to the sea before or immediately after scale formation. Because most sockeye salmon live in fresh water for a year or more, few scales of these ages are collected; they are usually in the 3_1 and 4_1 age groups.

Examples of these age groups are shown:

Age group 2_1. (0.1) one winter in the ocean zone. Spawning fish are "jacks."

Age group 3_1. (0.2) two winters in the ocean zone.

Age group 4_1. (0.3) three winters in the ocean zone.

Age group 5_1. (0.4) four winters in the ocean zone.

AGE GROUPS WITH ONE GROWING SEASON IN FRESH WATER (Plate 13)

These age groups make up many of the important runs of sockeye salmon. From the Columbia to the Copper River, and in the Wood River-Nushagak system in Bristol Bay, fish with this fresh-water history predominate every year.

Fish of a given year class may first be present in a spawning run as age group 3_2 ("jacks"); dominate the run the next year as age group 4_2 and (in some areas) the following year as age group 5_2; and provide occasional 6_2's and 7_2's in subsequent years. Thus, it is possible that fish of a year class with one growing season in fresh water could be present in the spawning migration over a 5-year period, but in most areas the period lasts only 3 or 4 years.

Examples of the following age groups are shown:

Age group 2_2 (1.0). One winter in fresh water, none in the ocean. (This illustration is from an immature fish, not an adult.)

Age group 3_2 (1.1). One winter in fresh water, one in the ocean.

Age group 4_2 (1.2). One winter in fresh water, two in the ocean.

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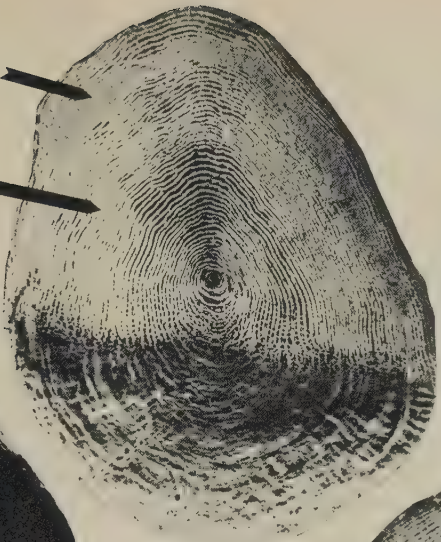
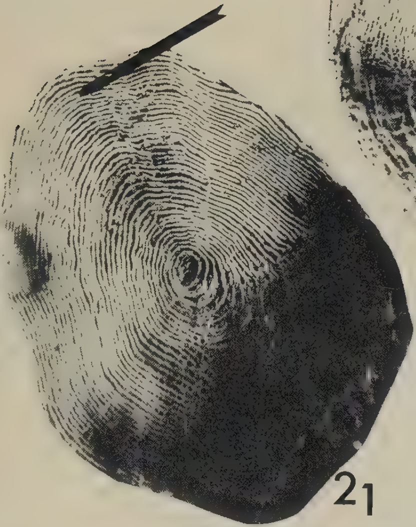
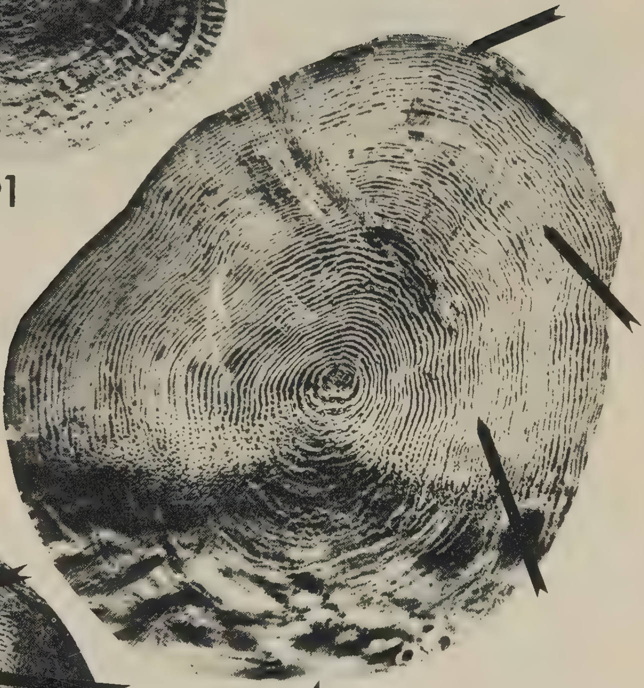
[11] Occasionally the small females in the Columbia River are called "jennies."



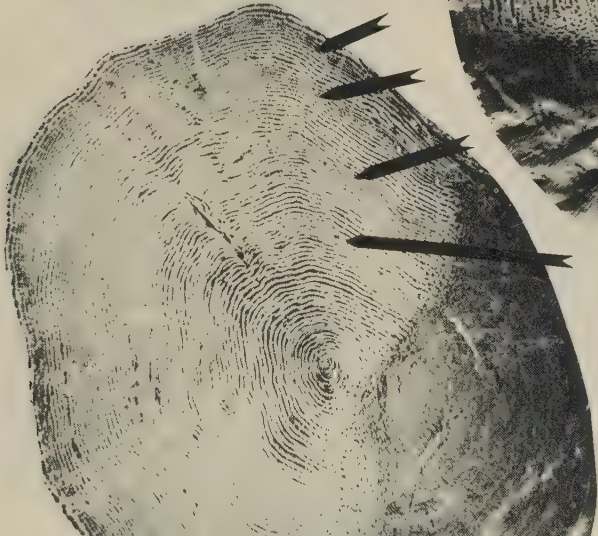
3_1



2_1



4_1



5_1

Plate 12.—Age groups with no scale growth in fresh water.

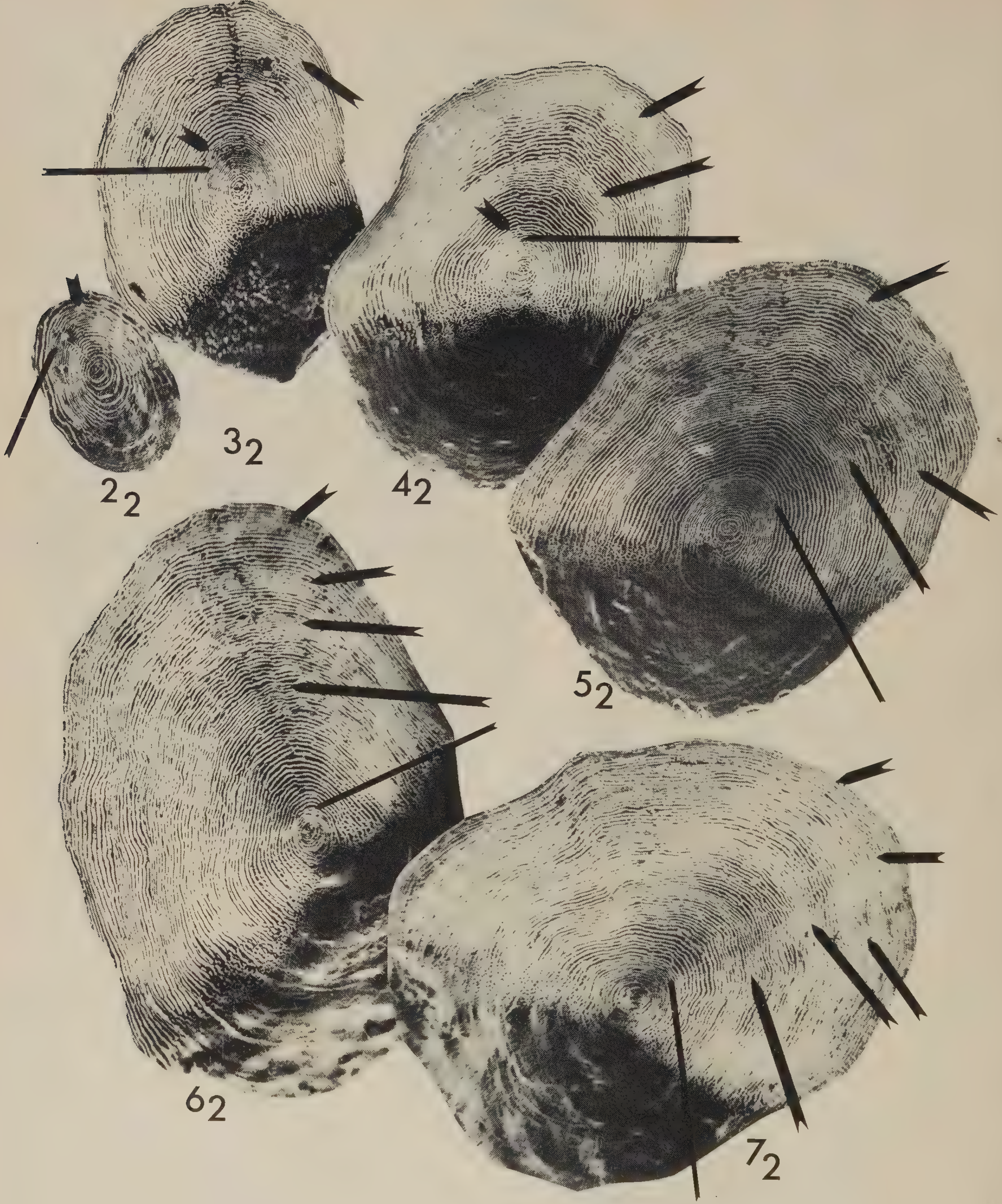

2_2
3_2
4_2
5_2
6_2
7_2

Plate 13.—Age groups with one growing season in fresh water.

Age group 5_2 (1.3). One winter in fresh water, three in the ocean.

Age group 6_2 (1.4). One winter in fresh water, four in the ocean.

Age group 7_2 (1.5). One winter in fresh water, five in the ocean.

AGE GROUPS WITH TWO GROWING SEASONS IN FRESH WATER (Plate 14)

These age groups also make up many important runs of sockeye salmon. The Ozernaia River in Asia, a number of tributaries of Bristol Bay, and Karluk River on Kodiak Island are areas where fish of these age groups predominate in the spawning runs in most years. Fish of a given year class may be in the spawning run one year as age group 4_3 ("jacks"); dominate the run the next year as age group 5_3 and (in some areas) the following year as 6_3's; and produce an occasional 7_3 the following year.

Examples of the following age groups are shown:

Age group 3_3 (2.0). Two winters in fresh water, none in the ocean. (This illustration is from an immature fish, not an adult.)

Age group 4_3 (2.1). Two winters in fresh water, one in the ocean.

Age group 5_3 (2.2). Two winters in fresh water, two in the ocean.

Age group 6_3 (2.3). Two winters in fresh water, three in the ocean.

Age group 7_3 (2.4). Two winters in fresh water, four in the ocean.

AGE GROUPS WITH THREE GROWING SEASONS IN FRESH WATER (Plate 15)

Fish of these age groups are common in the Karluk River, Alaska, and in some Asian areas. In some years they may make up a substantial portion of the spawning runs in these areas, primarily as age groups 6_4 and 7_4. Examples of the following age groups are shown:

Age group 4_4 (3.0). Three winters in fresh water, none in the ocean. (This illustration is from an immature fish, not an adult.)

Age group 5_4 (3.1). Three winters in fresh water, one in the ocean.

Age group 6_4 (3.2). Three winters in fresh water, two in the ocean.

Age group 7_4 (3.3). Three winters in fresh water, three in the ocean.

Age group 8_4 (3.4). Three winters in fresh water, four in the ocean.

AGE GROUPS WITH FOUR GROWING SEASONS IN FRESH WATER (Plate 16)

In areas where fish with three growing seasons in fresh water are common, occasional fish stay in fresh water another year. These fish are rare. Examples of the following ages are shown:

Age group 6_5 (4.1). Four winters in fresh water, one in the ocean.

Age group 7_5 (4.2). Four winters in fresh water, two in the ocean.

Age group 8_5 (4.3). Four winters in fresh water, three in the ocean. This group is very rare.

SCALES WITH IRREGULAR OR DEFORMED FEATURES

Some scales are of little or no value for age or racial study because they are regenerated (plate 17). Others may be unsuited for these studies because of resorption (plate 18), or for a number of other reasons (shown in plate 19).

REGENERATED SCALES (Plate 17)

When a salmon loses a scale, a new one rapidly replaces it.[12] The new scale does not form circuli until it approximates the size of the scale that was lost. Normal scale growth then resumes, and circuli form regularly thereafter. Regenerated areas range from a small portion of the center of the scale to almost the complete scale. When a scale is lost from large fish, the resulting regenerated scale is often of atypical size and shape.

Scales that were regenerated before the fish migrated to the sea can be used to determine the

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[12] Unpublished results of my experiments a few years ago showed that lost scales of coho (*O. kisutch*) and chinook (*O. tshawytscha*) salmon were replaced and had resumed normal growth within 1 month, even in fish which were in poor physical condition.

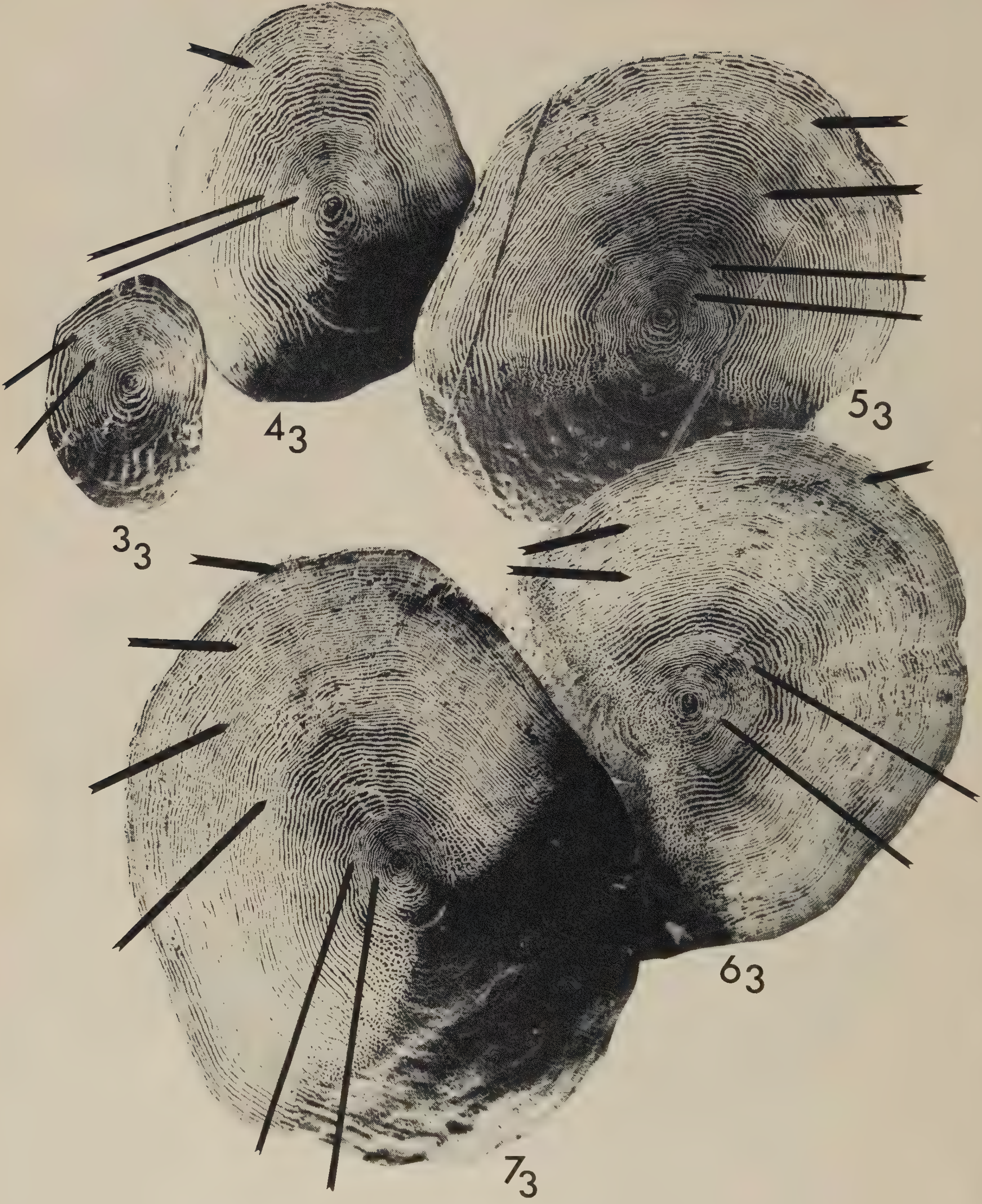
3_3
4_3
5_3
6_3
7_3

PLATE 14.—Age groups with two growing seasons in fresh water.

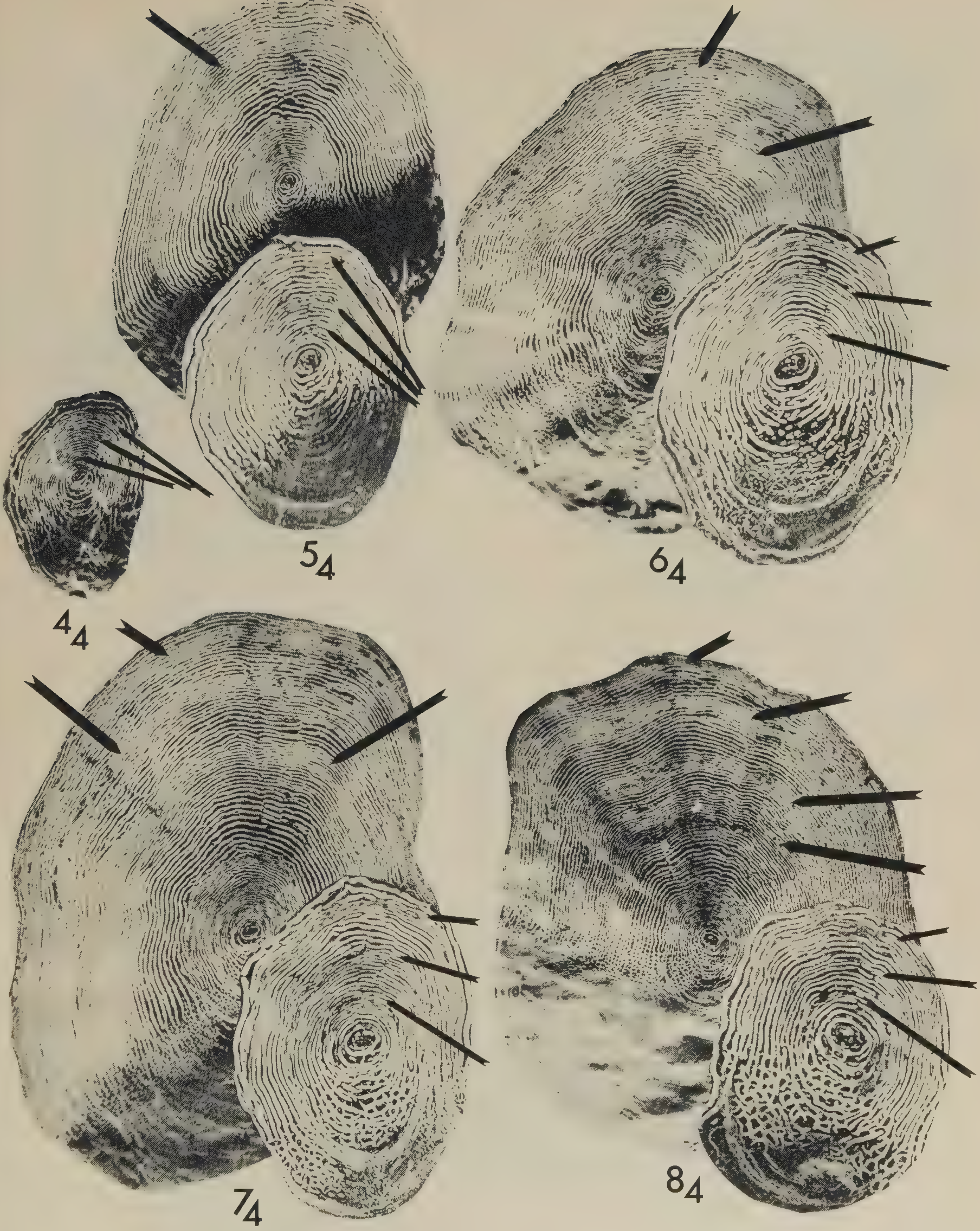

Plate 15.—Age groups with three growing seasons in fresh water.

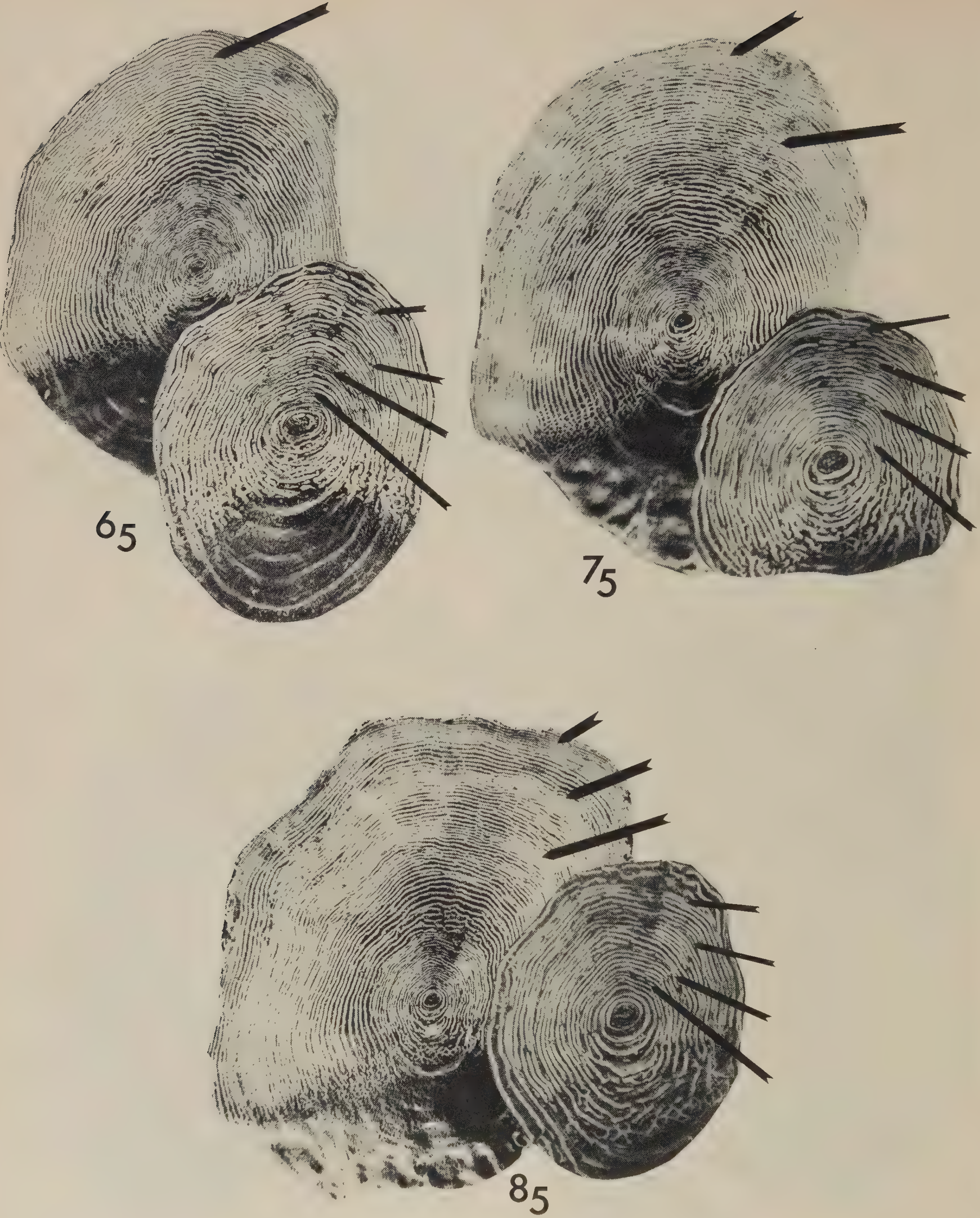

PLATE 16.—Age groups with four growing seasons in fresh water.

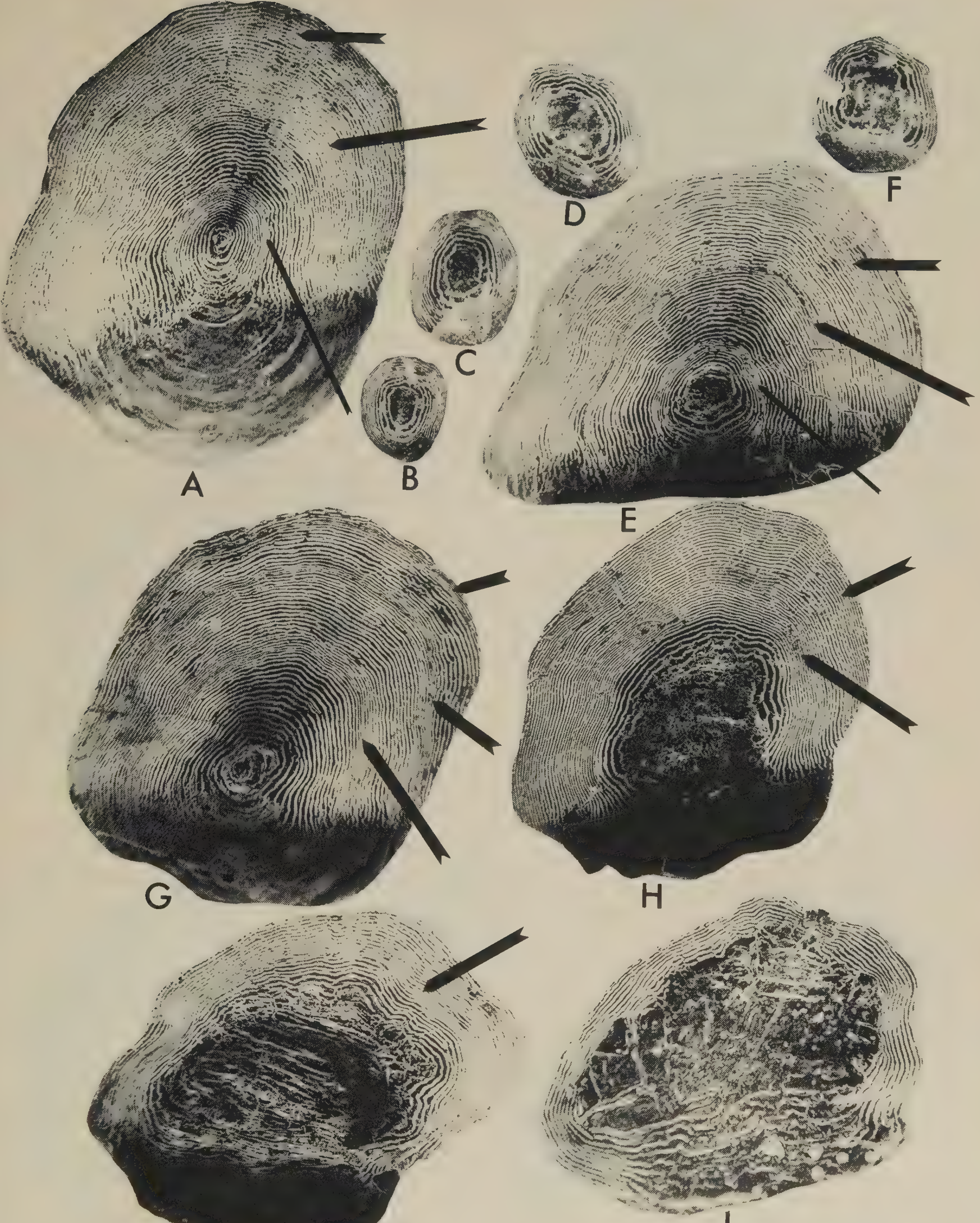
A
B
C
D
E
F
G
H
I
J

PLATE 17.—Regenerated scales.

ocean age of the fish, but only those that were replaced before the first winter reveal the total age.

Regenerated scales may be used to back-calculate the year of scale loss; for instance, scales taken from scars on the body of the fish may show the number of years since the injury. This technique can be applied to fish with gill net marks.

The scales on plate 17 are arranged to show increasing amounts of regeneration. Figures A and B, D and E, and F and G are pairs; the large scale of each pair shows about the same amount of regeneration of the fresh-water zone as the small scale of the pair. To illustrate how regenerated scales may be used to date an injury that removed the original scale, I arbitrarily assume that all the scales from adult fish on this plate were collected in the summer of 1965.

Scale A. A scale from an adult sockeye salmon shows regeneration of only a few central circuli; the fish spent one winter in fresh water and two winters in the ocean. This scale replaced one lost in 1962, a short time after the original scale was formed.

Scale B. A scale from a young sockeye salmon taken in fresh water shows regeneration that involves only a few circuli. At adult size the scale of this fish would look much like scale A.

Scale C. A scale from a young sockeye salmon. This scale shows a larger area of regeneration.

Scale D. A scale from a young sockeye salmon shows regeneration of about half of the scale.

Scale E. A scale from an adult sockeye salmon shows regeneration that involves about half of the fresh-water zone (scale D). This scale shows that the fish spent two winters in the sea and at least one in fresh water. This fish also lost the original scale in 1962; the age of the fish at that time could have been from a few months to over a year. The total age of the fish cannot be determined from this scale.

Scale F. A scale from a young sockeye salmon shows regeneration of most of the scale.

Scale G. A scale from an adult sockeye salmon shows regeneration of the entire fresh-water zone (scale F). This scale shows only that the fish spent three winters in the ocean and that the scale replaced one lost in 1962.

Scale H. A scale from an adult sockeye salmon shows regeneration of fresh-water growth and most of the first summer at sea. This scale shows that the fish spent two winters at sea after it lost the original scale in the summer of 1963.

Scale I. A scale from an adult sockeye salmon with only the winter and last summer's growth completed before capture. Because of extensive regeneration, even the ocean age of this fish cannot be determined. The scale is of slightly atypical shape; it replaced one lost in the summer of 1964.

Scale J. A scale from an adult sockeye salmon with only a few months' growth complete. The scale is atypical in size and shape; it replaced one lost in the spring of 1965 and is unusable for age or racial studies.

RESORBED SCALES (Plate 18)

At some time during the migration toward their spawning streams, sockeye salmon stop feeding and subsist on stored fat and other body materials. As they work their way up the streams, the material in the scales is resorbed. Resorption generally starts along the lateral margins of the scale near the base of the anterior field and progresses until the whole scale margin is affected. Scales taken from spawning fish may have only a small central portion left. On most resorbed scales taken from spawning fish the fresh-water growth may still be present, but usually the ocean growth zones are too badly eroded to permit determination of total age with confidence. With greatly resorbed scales, study of otoliths or length frequencies may be required to estimate the age of the fish.

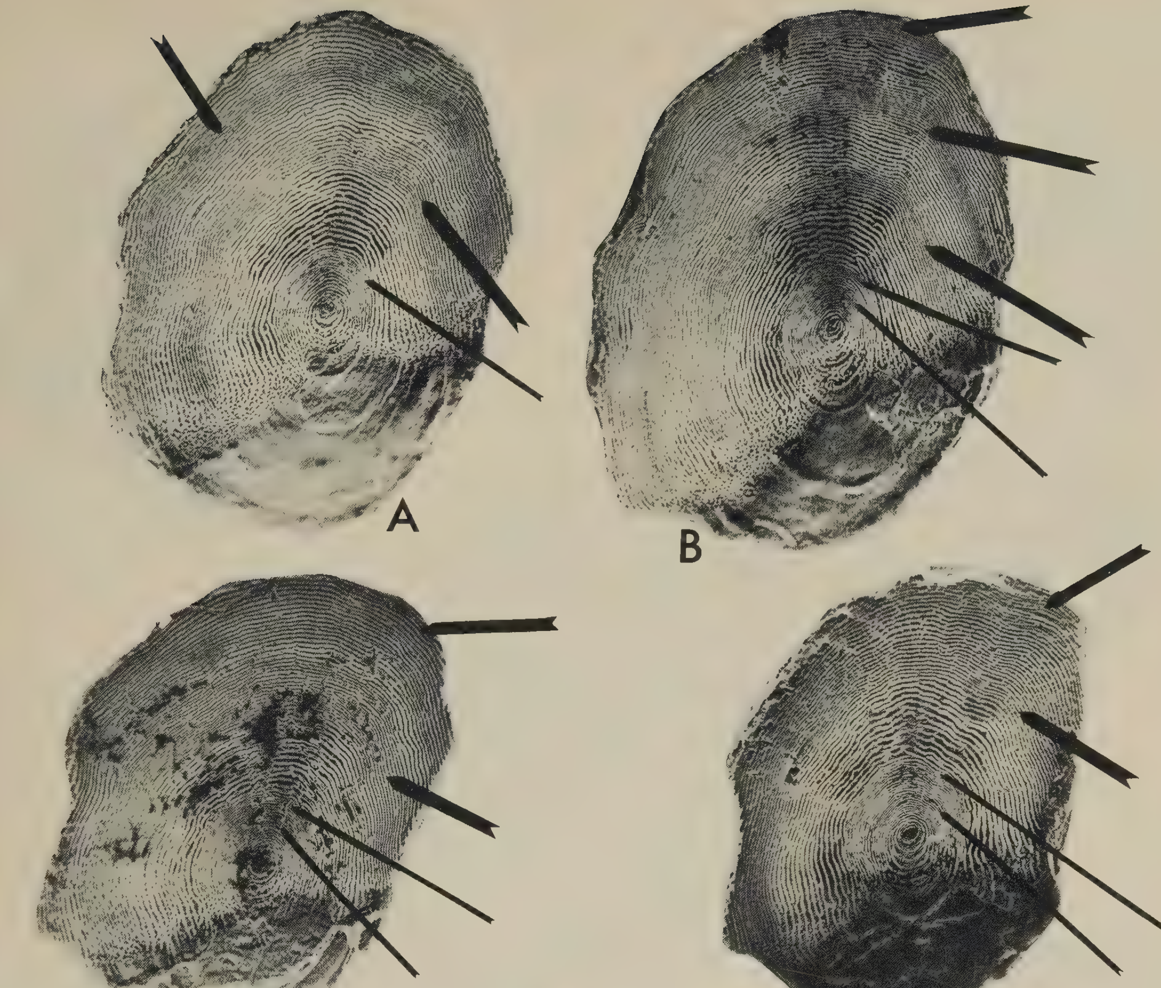

PLATE 18.—Resorbed scales.

The scales on this plate are arranged to show increasingly greater degrees of scale resorption, from A to H.

Scales A and B. These scales show slight resorption. Age determination is possible with these scales.

Scales C and D. These scales show considerable resorption. Age determinations are subject to error.

Scale E. This scale shows a greater amount of resorption than scales C and D, age determination is subject to considerable doubt.

Scales F and G. Only the fresh-water growth and a portion of the first year's ocean growth of these scales remain. Determination of total age is not possible.

Scale H. This scale shows considerable resorption and a regenerated center; it is useless for age or racial studies.

OTHER SCALES NOT SUITED FOR AGE OR RACIAL STUDIES (Plate 19)

Scales can be unusable for a number of reasons other than regeneration or resorption, as shown by the following examples:

Scale A. Scales may be distorted with atypical sculpturing. These scales often adjoin regenerated scales.

Scale B. Scales of adult and young fish may have a twisted center or other distorted area. If the growth pattern is not too badly distorted, the correct age may be determined from the scale.

Scale C. Scales may have scars (arrow). Here again, if the damage is not too serious, the correct age may be determined. Scars are more common in the ocean growth zones than in the fresh-water zone—perhaps because the scales of small fish are more easily lost than displaced in the scale pocket.

Scale D. Scales from the lateral line have a trough or tubelike structure that forms part of the lateral line organs. Scales near the lateral line may also be distorted to a varying degree, but some may be usable.

Scale E. Scales of atypical size and shape occur near the bases of the fins and the operculum; they should not be used for age or racial studies as they usually have fewer circuli than preferred scales.

USE OF ATLAS

Now that we have examined the features of sockeye salmon scales in detail, we are ready to use the atlas for specific purposes. This section is divided into two parts: (1) The use of the atlas in age studies and description of the scale features and (2) the use of the atlas in racial and other studies.

USE OF THE ATLAS FOR AGE STUDIES AND DESCRIPTION OF IMPORTANT SCALE FEATURES

This section demonstrates the use of the atlas to describe the physical features of the scale and to determine the fresh-water, ocean, and total age of the sockeye salmon from its scales. Compare the scale being studied with the plates in sequence, starting with plate 3. Compare the individual features of the scale with the variations shown on the appropriate reference plate. Select the one that is most similar to the feature under study.

The scale shown in plate I is used here to illustrate this method. Compare the scale in plate I with the various reference plates as follows:

Plate 3. Column A, chiefly regular, unbroken circuli.

Plate 4. First winter zone in the fresh-water growth is of type 1, sharp, the second is of type 2, moderately sharp.

Plate 5. Fresh-water age 2., medium-sized zone.

Plate 6. A sharp transition from fresh-water growth to ocean growth without plus growth. Type A (like fig. 1).

Plate 7. First ocean growth zone is of type 1; circuli are chiefly unbroken and uniformly spaced. Second ocean growth zone is of type 2, "average."

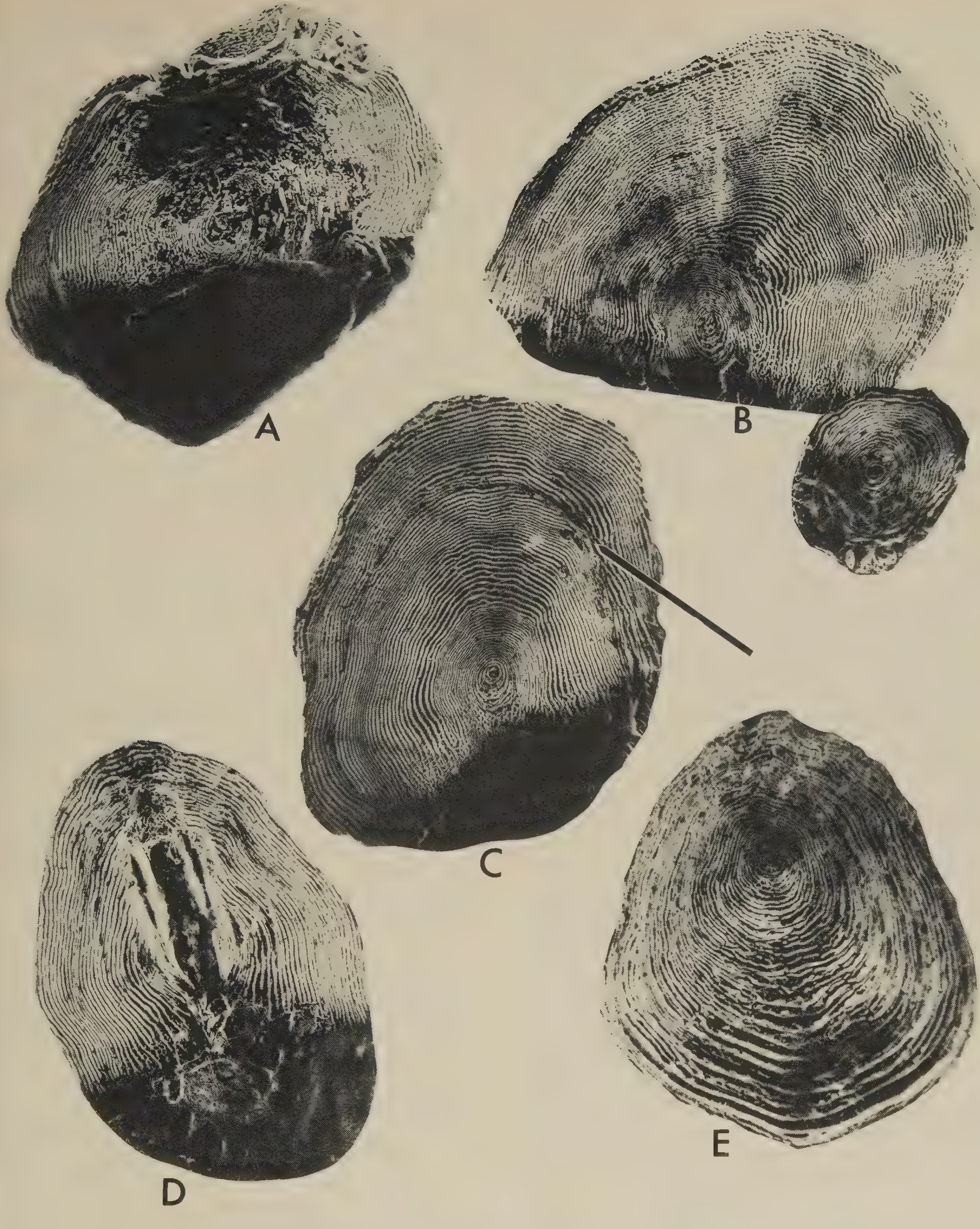

Plate 19.—Other scales not suited for age or racial studies.

Plate 8. The first ocean zone has 24 circuli; the second has 21.

Plate 9. The widest spaced circuli of the first ocean zone are near the fresh-water growth; in the second ocean zone, they are near the previous winter zone.

Plate 10. Both ocean winter zones are of type 2, "average."

Plate 11. This fish is ocean age .2.

Plates 12 to 16. This fish is of age group 5_3 (2.2), shown on plate 14.

USE OF ATLAS FOR RACIAL AND OTHER STUDIES

Numerous scale characters are being used to determine the continent of origin of sockeye salmon when they are caught away from natal streams. Some scale characters and methods of analysis were reported by Krogius, 1958; Kubo, 1958; Kubo and Kosaka, 1959; Henry, 1961; Mosher et al., 1961; Anas, 1963; Mosher, 1963; and Anas, 1964. Methods now under study to determine the stream of origin range from identification based on appearance of the scale to multivariate techniques that make use of scale data collected with precision. Although numerous characters have been examined for racial studies, many more could be defined and used; some of the additional characters might be better than ones now in use.

This atlas can be used to (1) find additional characters for racial study, (2) decide which circuli or parts of circuli to count or measure for consistent results, (3) provide a basis for developing "standard" descriptions of the scale characters of sockeye salmon from the different spawning regions of North America and Asia, and (4) choose characters for special studies in which data on sockeye salmon scales are used.

No specific list of additional characters is given here, but ingenuity and imagination of the scientist in discovering and developing use of scale characters and methods of analysis will open new possibilities for the study of sockeye salmon.

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APPENDIX A

GLOSSARY OF TERMS

Adventitious mark or check.—A nonperiodic interruption in the regular pattern of scale growth. The check may or may not resemble a winter growth zone. See plates 6 (migration checks), 19B (twisted areas), and 19C (scar).

Annual ring, annulus, resting zone, winter ring, winter zone, winter mark, year mark, or year ring.*—A concentration of circuli or a series of interrupted circuli denoting a winter of life of the fish. See plates 1, 4, and 10.

Annulus.—See annual ring and footnote 4.

Anterior field, sculptured field.*—The portion of the scale that was embedded in the scale pocket toward the head of the fish and is sculptured with circuli. See plate 1. All plates show anterior fields.

Bases of circuli.—On the sockeye salmon scale only the first few circuli encircle the center or focus of the scale. The circuli beyond these first few are arcs. The ends of the circuli at the posterior field are their bases.

Central platelet or focus.—The area enclosed by the first or central circulus.

Circulus (plural, circuli), stria, or sclerite.*—A ridge on the upper surface of the anterior field of the scale. See Neave (1936), Welander (1940), or Wallin (1957). The circuli and interspaces (grooves) appear under magnification as concentric light and dark rings around the anterior field of the scale. All plates show circuli.

Clear field or area, posterior field or area.*—The portion of the scale which protrudes from the scale pocket toward the tail of the fish. This portion of the scale is a relatively clear area without distinctive growth features. See plate 1.

Focus.—See central platelet.

Fresh-water growth, fresh-water zone, fresh-water growth zone, lacustrine growth, lacustrine zone, lacustrine growth zone, or nucleus.*—The central portion of the scale formed while the fish was in fresh water. See plates 1 and 3 through 5.

Incidental growth, incidental zone, incidental growth zone, intermediate growth, intermediate zone, intermediate growth zone, plus growth, plus zone, plus growth zone, transitional zone, transitional growth zone, transitional zone, or spring growth.*—The portion of some scales between the fresh-water and the ocean growth zones where the difference between the fresh-water and ocean type circuli is not clear. See plate 6.

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* here and later indicates the term I prefer.

Intercirculus space, interspace.—A groove between two circuli. See circuli.

Intermediate growth, intermediate zone, intermediate growth zone.—See incidental growth zone.

Interspace.—See intercirculus space.

Lacustrine growth, lacustrine zone, lacustrine growth zone.—See fresh-water growth.

Marine growth, marine zone, marine growth zone, ocean growth, ocean zone, or ocean growth zone.*—The portion of the scale formed while the fish was in the ocean. See plates 1 and 7 through 11.

Migration check. — An adventitious check formed on some scales at the end of the incidental or plus growth. See plate 6.

Nucleus.—See fresh-water growth.

Ocean growth, ocean zone, ocean growth zone.*—See marine growth.

Plus growth, plus zone, plus growth zone.*—See incidental growth.

Posterior field or area.*—See clear field.

Regenerated scale.—A scale that replaces one that has been lost. The new scale grows without the formation of circuli until it reaches the approximate size of the scale which was lost. See plate 17.

Resorbed or eroded scale.*—A scale with the margins eroded because of sexual maturation. See plate 18.

Resting zone.—See annual ring. This term is often used by Japanese scientists.

Scar.—An abrupt change in the regular pattern of scale growth marked by a displacement of the natural configuration of the circuli. See plate 19C.

Sclerite.—See circulus. This term is widely used in Europe.

Sculptured field or area.—See anterior field.

Spring growth or spring growth zone.—See incidental growth and footnote 8.

Stria.—See circulus.

Transition zone, transitional growth, transitional growth zone, transition zone.—See incidental growth.

Winter ring, winter mark, or winter zone.*—See annual ring.

Year mark or year ring.—See annual ring.

APPENDIX B

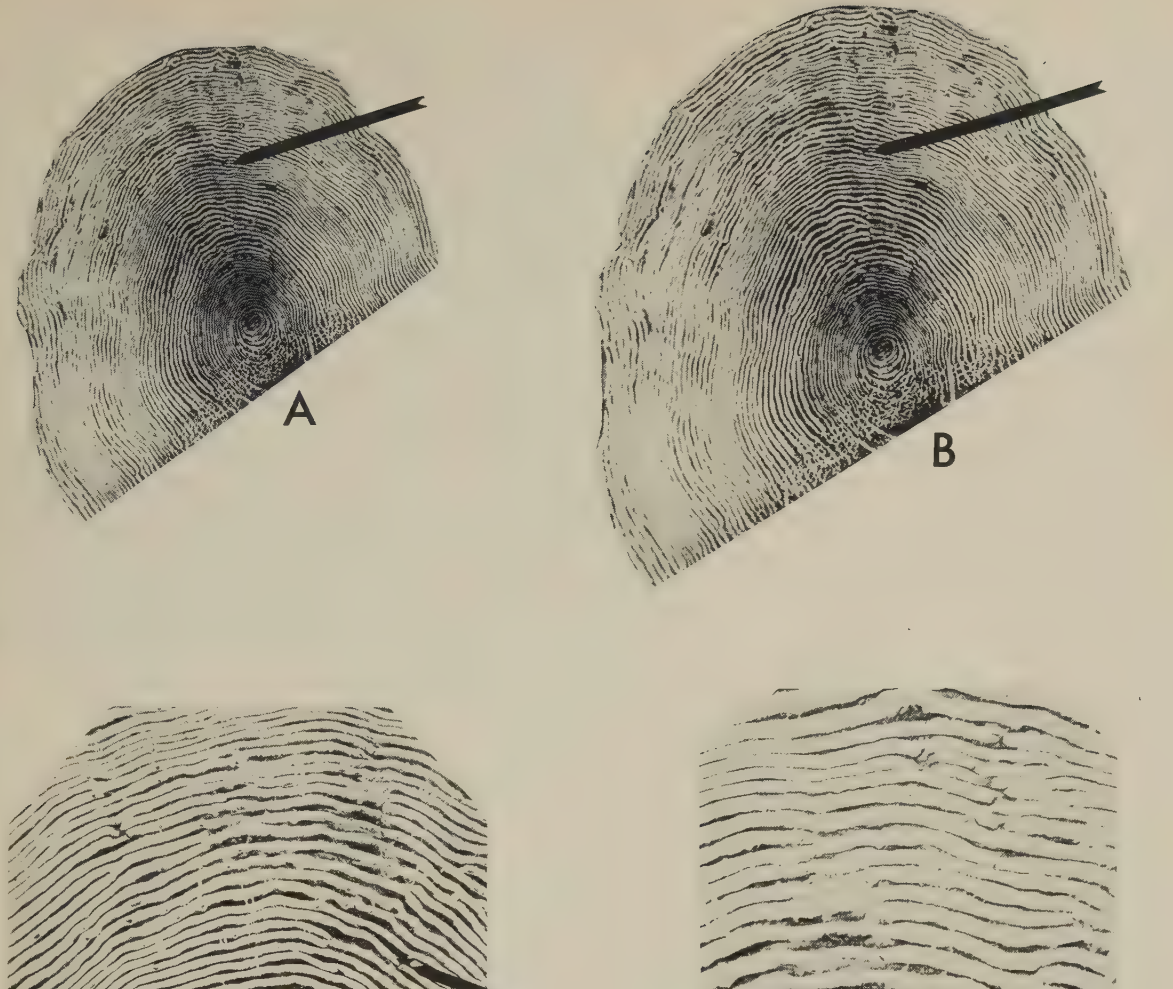
EFFECT OF MAGNIFICATION ON APPEARANCE OF SCALE FEATURES (Appendix Plate 1)

The magnification which should be used for examination of scales from sockeye salmon varies with the size of the scales, the intended use of the data, and the preference of the scientist. The photographs in appendix plate 1 show how features of sockeye salmon scales appear at different magnifications and indicate the relative magnifications for various scale studies. (The arrows indicate the same feature on each scale section.)

Scale sections (shown at various magnification) follow:

Section A.	About 19 X. Note how difficult it is to identify any of the scale features on this photograph.
Section B.	About 25 X. Note that the ocean winter zones are distinct at this magnification, but the fresh-water features are difficult to determine.
Section C.	About 50 X. The ocean winter zones are less distinct at this magnification, but the details of the fresh-water zone are clear.
Section D.	About 100 X. The ocean winter zones are very difficult to identify and delimit at this magnification.

Thus, the scales should be studied first at a magnification of between 25 X and 50 X to observe the whole scale in perspective and the details of the ocean zone. Then a magnification of between 50 X and 100 X should be used for the fresh-water zone, counts, and measurements of circuli, . . . These ranges of magnification are suggested as a starting point, because the exact magnification needed depends on the use of the data and on the temperament and visual habits of the investigator.



APPENDIX PLATE 1.—Effect of magnification on appearance of scale features.

APPENDIX C

APPEARANCE OF SCALES AND SCALE IMPRESSIONS (Appendix Plate 2)

Impressions of scales in plastic offer a number of advantages over the use of the scales themselves:

1. The effect of dirt on the scales is minimized—especially dirt on the unsculptured surface.
2. Duplicates can be made that are exact copies of the scales.
3. Impressions are easier to file and store than scales mounted on glass slides and the chance of breakage is reduced.

The process of making plastic impressions was described by Clutter and Whitesel (1956) and by Koo (1962a). Impressions made with a cold roller are not as satisfactory for salmon scales as those made with the heat-press method. (In 1955, a series of salmon scale impressions made with a jeweler's cold roller were compared with those made with a heat press. The heat-press impressions were greatly superior.)

In appendix plate 2, scale A shows a section of a sockeye salmon scale, and scale B shows an impression of the same scale section. The photograph of the impression shows slightly sharper circuli with less fuzziness from dirt and foreign material on the surface of the scale. Note that the photograph of the impression was reversed for comparison.

APPENDIX D

APPEARANCE OF NEGATIVE AND POSITIVE PRINTS (Appendix Plate 3)

When plastic impressions are made of the scales, the ridges on the scale surface become valleys in the impressions. Koo and Finn (1964) found that the sharp troughs of the impressions and the ridges on the scales both appear as dark rings when examined by transmitted light. When either the scale or its impression is examined by reflected light, these structures appear as light rings. Because the circuli and adjoining interspaces over much of the scale have about the same width, and because some workers project the scales by transmitted light and others use dark-field techniques for direct microscopic examination, it makes little difference whether the scale photograph is a positive or a negative print.

In appendix plate 3 there is an example of each type: Scale A is a positive print and scale B a negative print of the same sockeye salmon scale.

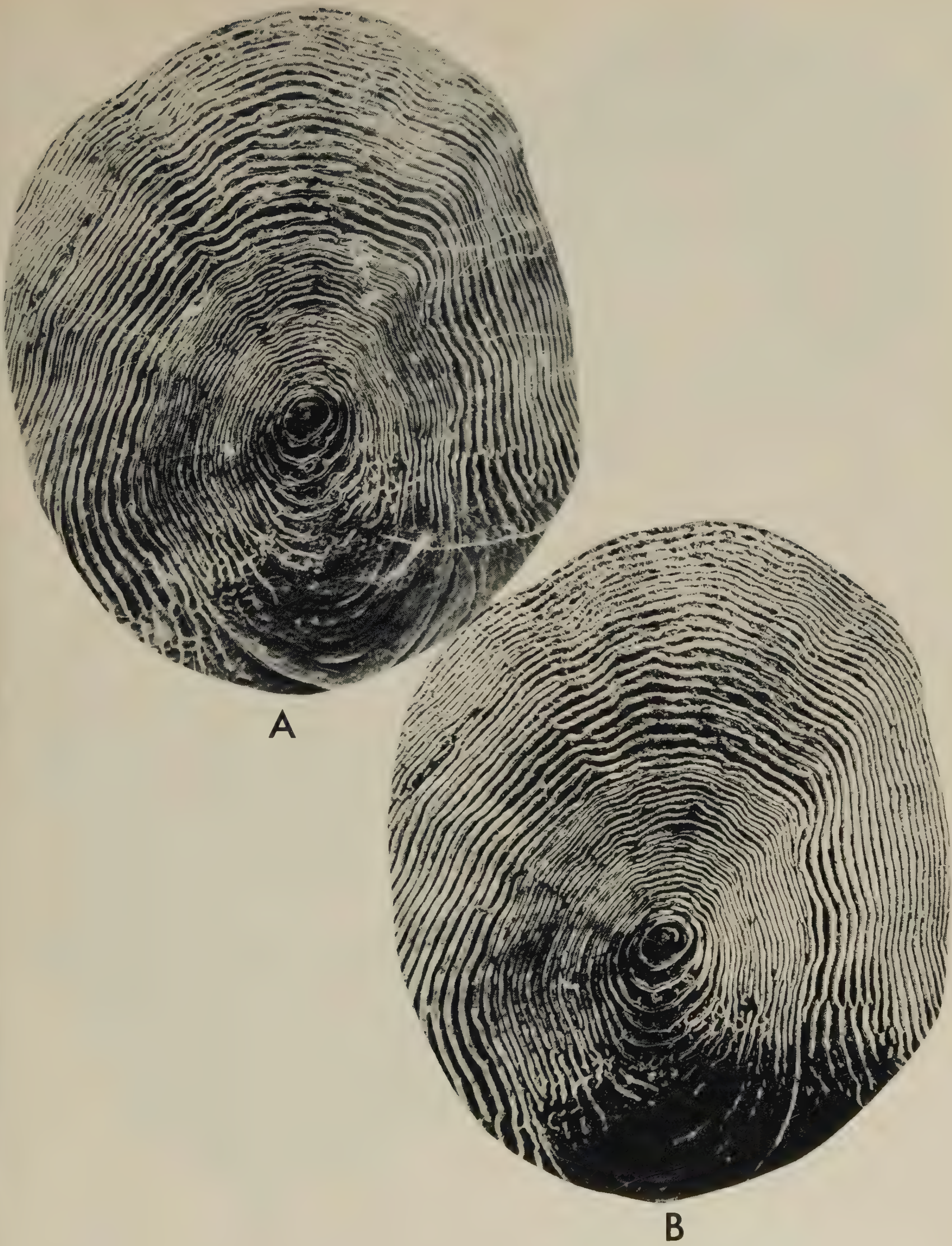
The only real difference in the prints is in the posterior field where growth features are absent anyway. The density of the negative print more nearly matches the image seen under the projector, or through the microscope; negative prints, therefore, were used in making this atlas.

APPENDIX E

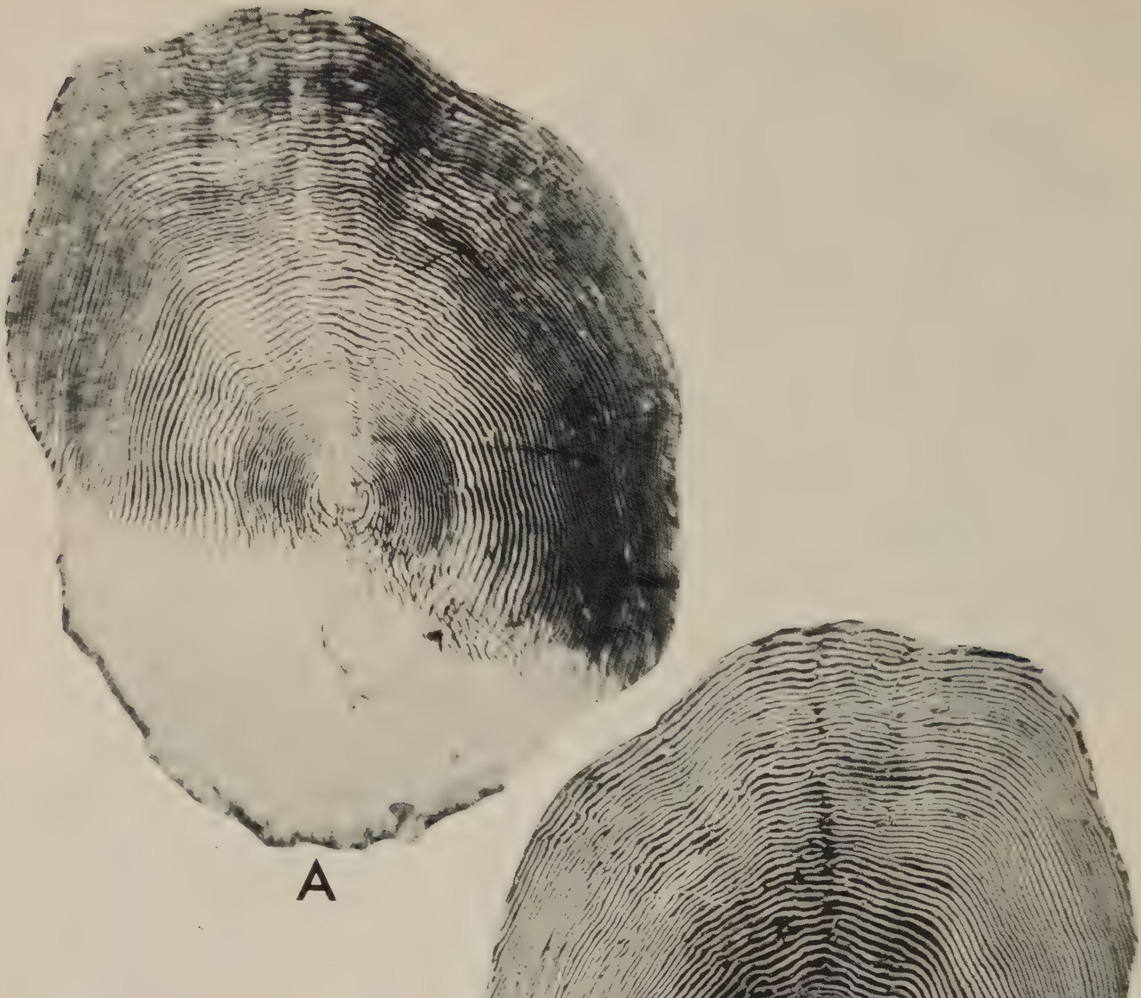
TECHNIQUES OF PHOTOGRAPHING SCALES

The scales were photographed by placing a piece of high-contrast photographic enlarging paper under the image from a scale projector set up in a darkroom. The image was first carefully focused on a white paper in a printing frame. Then, with only a darkroom safelight on, a piece of the enlarging paper was substituted for the focusing paper, exposed, developed in a high-contrast paper developer (minimum exposure-maximum development), and fixed, washed, and dried in the usual manner.

Positive prints can be made by taking a picture of a scale with a microscope camera (a single lens reflex camera on a microscope), or by photographing the projected image with a camera, then exposing and processing the same as for any photograph of a high-contrast subject.



Appendix plate 2.—Appearance of scales and scale impressions.



APPENDIX PLATE 3.—Appearance of negative and positive prints.

GROWTH OF JUVENILE BLUE CRABS, *Callinectes sapidus* RATHBUN, IN THE ST. JOHNS RIVER, FLORIDA

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ABSTRACT

Relative growth was studied by holding juveniles (20–139 mm. wide) in anchored floats. The floats were at two locations—one in salt water and one in fresh water. Molt intervals were similar at both sites, but the average growth was generally more per molt in salt water. From April to mid-November, the mean molt interval was 11 days for crabs 20 to 29 mm. wide; it increased to 41 days for crabs of 130 to 139 mm. Frequency of molting decreased in winter, but most juveniles 20 to 59 mm. wide molted two or three times. Growth increments per molt varied from 7.8 to 50 percent. Mean increment, by 10-mm. width groups, was 20.9 to 34.2 percent. Estimates of increase in width with age indicate that most blue crabs in the St. Johns River reach harvestable size (width of 120 mm.) within 1 year after hatching.

This report presents the results of studies from April 1964 to March 1966 on growth increments, molt intervals, and the effects of salinity and temperature on growth of juvenile blue crabs, *Callinectes sapidus* Rathbun, in the St. Johns River, Fla. This information on growth is needed to estimate the time required for crabs of any particular size to reach harvestable size.

Because the juvenile (postlarval) crab has a rigid shell, it can grow only when it molts. The shell is composed of chitin strengthened by the deposition of calcium salts (Rees, 1963). Before molting, the crab forms a new exoskeleton inside the old shell, which then loosens. During molting, the carapace separates from the abdomen along the sides of the undersurface, and in a few minutes, the crab backs out of the old shell (fig. 1). Initially, the new shell is soft and wrinkled. Water, absorbed after molting, stretches the thin and elastic new cuticle and increases the size of the crab. Crabs grow from the first postlarval crab stages, about 2.5 mm. wide, to full size after 18 to 23 molts (Van Engel, 1958). In the St. Johns River, the width of fully grown blue crabs ranges from less than 100 mm. to more than 240 mm.

Few studies have been made on the rate of growth of juvenile blue crabs. Churchill (1919) used the limited number of molting records available at that time for Chesapeake Bay crabs and attempted to determine size at various instars and the frequency of molting from hatching to maturity. He found that time between molts was progressively longer with increase in size. The first few molts were a few days apart and the last at intervals of a month or more. He reported that growth ceases from October until late April or early May and that the animals probably do not molt at temperatures less than 60° F. (15.5° C.). Studies with blue crabs over 29 mm. wide by Gray and Newcombe (1938) and on smaller crabs by Newcombe, Sandoz, and Rogers-Talbert (1949) provide the best published data on growth. The mean increases in width of the various instars ranged from 15 to 48 percent; the mean was 25 percent for males and 27 percent for females. No information was obtained on molt intervals because the animals were held for only one molt.

Numerous reports of unusually large blue crabs in low-salinity waters and very small adult crabs in high-salinity waters suggest a possible negative correlation of size with salinity of the water in which growth occurs (Newcombe, 1945; Porter, 1956; Cargo, 1958; Fischler, 1959; Tagatz, 1965). Van Engel (1958) believed that crabs in low salinity absorb more water at the time of the molt and, thus, increase more in size than crabs that molt in water of higher salinity.

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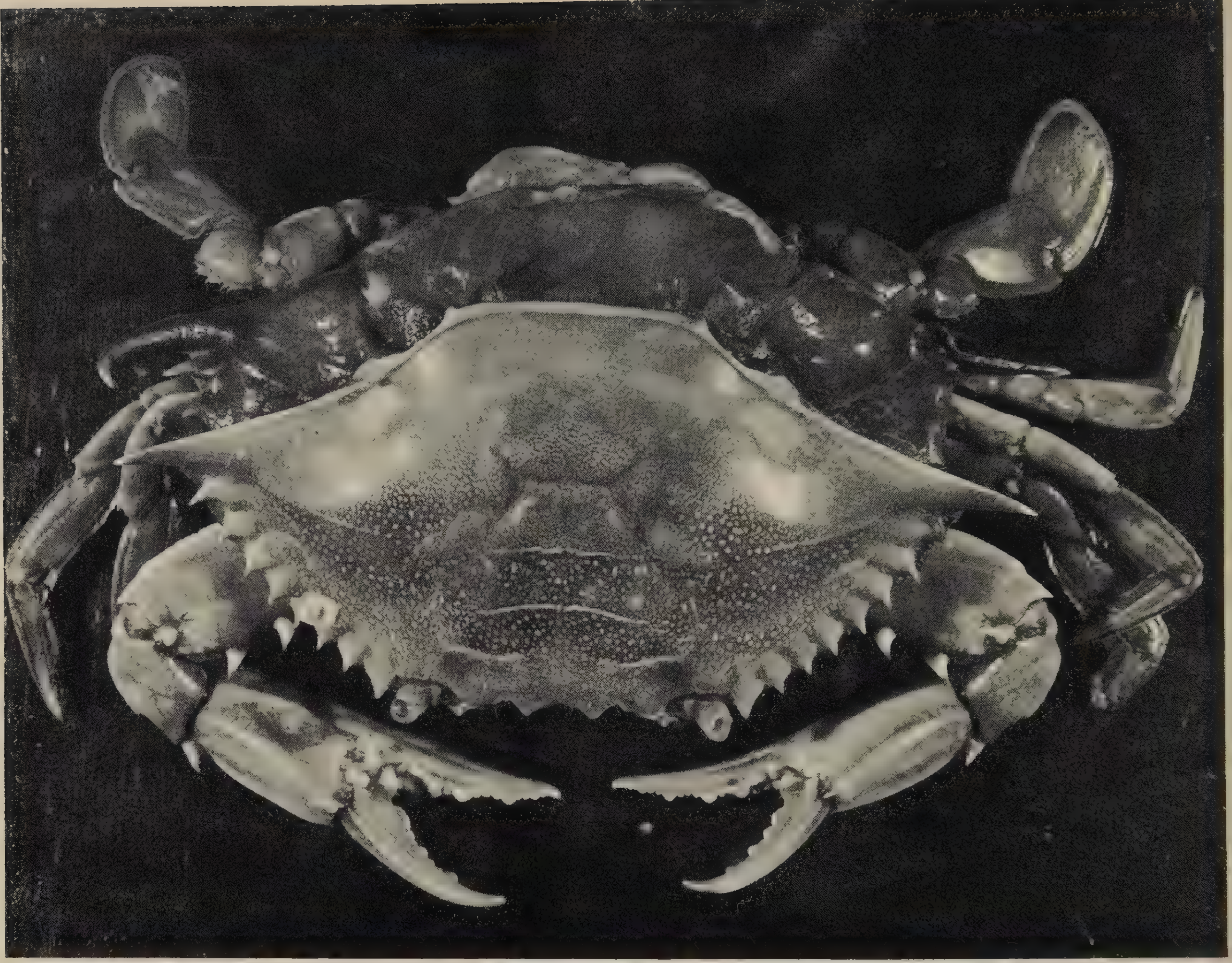

FIGURE 1.—A molting blue crab emerging from its old shell.

MATERIALS AND METHODS

Juvenile blue crabs, 20 to 139 mm. wide, were held in wooden floats in salt water (salinity greater than 5 p.p.t.—parts per thousand) from April 1964 to March 1965 and in fresh water (salinity less than 1 p.p.t.) from April 1965 to March 1966. Studies in salt water were in Cedar Point Creek, a tidal tributary of Clapboard Creek, which enters the St. Johns River 15 km. from the Atlantic Ocean. Studies in fresh water were in the St. Johns River near Green Cove Springs, 90 km. upstream from the mouth of the river. Both sites were natural habitats for crabs in the size range used.

Two hundred crabs in four floats were used at each location. The floats had hinged covers and were about 3 m. long, 1½ m. wide, and ½ m. deep. A 15-cm.-wide rim allowed three-fourths of the float to hang submerged. Each float had 50 compartments, 24 cm. by 24 cm. by 46 cm. deep, covered with 6.4-mm.-mesh hardware cloth.

Blue crabs were collected near the floats, and only one animal was put in each compartment (to prevent cannibalism). About 2,000 of those captured were measured for length-width ratio.

Three times each week crabs were fed, those that had molted were measured, and the dead ones were removed. The crabs normally were supplied with more cut fish than they would eat. I measured carapace width and length of each animal that had molted since the last observation; shell hardness indicated the day of ecdysis. Width is the distance between the tips of the large lateral spines, and length the distance between the median anterior notch and the posterior margin. Measurements of crabs that died within a week after molting were not used in estimating growth. Except for length-width ratio, I discuss growth in terms of width.

Salinity and temperature were measured at each observation. Salinity determinations, obtained within 2 hours of low tide at Cedar Point Creek, probably were near minimum values for this site. Salinities at Green Cove Springs were always less than 1 p.p.t.—the lowest concentration detectable with the hydrometer. Blue crabs and other marine forms are able to live in the upper St. Johns River because it has a high concentration of calcium chloride and also localized areas of high sodium chloride (Odum, 1953).

I defined as summer studies those from early April to mid-November and as winter studies those from near the end of November through March. Summer work ended earlier in salt water because of damage to the floats from a September storm. During the summer, crabs were replaced (randomly collected near floats) when they died, escaped, attained maturity, or surpassed 139 mm. All new crabs were used at the start of winter, and none were replaced.

LENGTH-WIDTH RATIO

Length-width ratios were obtained for blue crabs 10 to 149 mm. wide captured in the St. Johns River (table 1). For comparison, I have included the data given by Newcombe et al. (1949) for Chesapeake Bay blue crabs. The two sets of data show similar changes in body form with growth. As size increases, the length-width ratio decreases. For St. Johns River crabs the ratio expressed as a percentage was 50 in juveniles 10 to 19 mm. wide and decreased to less than 42 in crabs over 119 mm. wide. In crabs over 69 mm. wide, males were proportionally longer than females.

The body proportions of blue crabs from the St. Johns River differed from those of crabs from the Chesapeake Bay. In every width class the Chesapeake Bay crabs had a greater mean length than the St. Johns River crabs. Geographic variation is to be expected in an animal as widely distributed as the blue crab.

TABLE 1.—*Length-width ratios of blue crabs from St. Johns River, Fla., and Chesapeake Bay*

Sex and width	St. Johns River				Chesapeake Bay[1]			
	Crabs	Mean width	Mean length	Length/width	Length/width	Mean length	Mean width	Crabs
Mm.	*Number*	*Mm.*	*Mm.*	*Percent*	*Percent*	*Mm.*	*Mm.*	*Number*
Males:								
10–19	10	16.8	8.4	50.0	53.2	9.2	17.3	13
20–29	67	25.4	12.5	49.2	53.3	13.6	25.5	17
30–39	130	34.7	16.4	47.3	49.7	17.7	35.6	16
40–49	122	44.1	20.7	46.9	49.4	22.4	45.3	27
50–59	88	54.4	25.3	46.5	48.6	26.5	54.5	32
60–69	69	63.9	29.3	45.8	48.5	31.7	65.4	35
70–79	69	74.7	34.6	46.3	47.5	35.3	74.3	31
80–89	93	83.8	37.7	45.0	46.9	40.1	85.4	37
90–99	65	94.4	42.2	44.7	47.2	44.2	93.7	39
100–109	54	103.8	45.3	43.6	46.2	48.3	104.6	38
110–119	52	114.9	49.4	43.0	45.7	52.7	115.3	37
120–129	52	124.2	51.5	41.5	46.2	57.9	125.3	32
130–139	46	133.8	54.3	40.6	44.8	60.2	134.4	35
140–149	22	145.0	59.0	40.7	44.9	65.4	145.7	42
Females:								
10–19	11	16.8	8.4	50.0	53.9	8.9	16.5	22
20–29	78	25.3	12.4	49.0	52.5	12.8	24.4	21
30–39	129	34.6	16.5	47.7	50.3	18.4	36.6	19
40–49	136	44.4	20.7	46.6	49.7	22.5	45.3	50
50–59	119	54.3	25.3	46.6	49.0	27.1	55.3	83
60–69	102	63.7	29.5	46.3	48.1	31.1	64.6	103
70–79	116	74.4	33.8	45.4	47.1	35.1	74.5	79
80–89	109	84.1	37.7	44.8	46.5	39.2	84.3	65
90–99	103	94.7	41.4	43.7	45.2	42.6	94.3	58
100–109	48	103.9	44.3	42.6	45.2	47.3	104.7	38
110–119	58	113.7	48.0	42.2	44.0	50.1	113.8	32
120–129	30	124.5	50.3	40.4	44.4	55.4	124.7	34
130–139	11	132.6	53.4	40.3	44.5	59.0	132.7	25
140–149	13	143.8	55.8	38.8	41.7	60.6	145.3	21

[1] Data from Newcombe et al. (1949).

RELATIVE GROWTH

Observations on growth were made during summer and winter.

SUMMER

I obtained data on 1,085 molts in salt water (April 1 to September 15, 1964) and on 1,152 in fresh water (April 24 to November 15, 1965).

Water temperatures were somewhat similar at the sites, but salinities differed by as much as about 26 p.p.t. The mean water temperature was 26.8° C. in salt water (range, 13.8°–32.1° C.) and 25.8° C. in fresh water (range, 16.2°–31.5° C.). Mean salinity (readings taken within 2 hours of low tide) at the Cedar Point Creek site was 18.8 p.p.t. (range, 7.5–25.8 p.p.t.); at Green Cove Springs, salinity was always less than 1 p.p.t.

Confinement did not appear to inhibit growth of blue crabs. The experimental animals ate readily, remained pugnacious, and many molted six or seven times. Growth increments of crabs that molted more than once in confinement averaged about the same as those for crabs of comparable size that molted only once.

Growth increments were highly variable in each size group, but no blue crab molted without some increase in size. The smallest increase in width was 7.8 percent; the largest, 50 percent. Mean percentage growth per molt by 10-mm.-width groups was 20.9 to 34.2 (table 2), and the groups averaged 26.7 for females, 23.9 for males, and 25.3 for females and males combined. Among larger crabs, females usually had greater width increments (at greater ages, they are relatively wider than male crabs). On the assumption of homogeneous variance about the regression of postmolt width on premolt width, an analysis of covariance indicated significant interaction of sex and salinity on growth ($P < 0.01$). Because of this interaction the separate effects of salinity on males and females were examined. Each sex showed significant differences in growth between fresh and salt water ($P < 0.05$). All crabs less than 80 mm. wide and many larger ones had greater average growth in salt water (fig. 2).

Some factor other than salinity appears to account for larger crabs in certain low-salinity waters. In the present experiments and in earlier ones on the terminal molt of female blue crabs (Haefner and Shuster, 1964), decrease in salinity did not produce increase in size.

Female blue crabs undergo a final molt at which they become sexually mature. This stage is easily recognizable because the abdomen changes shape from triangular to semicircular (the last stage of males cannot be determined from external appearance). In the St. Johns River, as in Chesapeake Bay (Tyler and Cargo, 1963), the sizes at the last two instars overlap widely. The smallest mature female measured was 99 mm. wide, and the largest immature female was 177 mm.

I obtained data on the terminal molt of 170 females (83–139 mm. wide)—85 at each site. Most growth generally took place at this molt. The mean increase in width was 34.4 percent (range, 19.6–50) in salt water and 30.2 percent (range, 20.5–47.4) in fresh water.

Table 2.—*Relative growth of blue crabs, by 10-mm.-width groups and by sex, in salt (S) and fresh (F) water, St. Johns River, Fla., April 1 to November 15, 1964 and 1965*

Width and habitat	Males			Females		
	Crabs	Mean increase and standard deviation	Range	Crabs	Mean increase and standard deviation	Range
Mm.	*Number*	*Percent*	*Percent*	*Number*	*Percent*	*Percent*
20–29						
S	17	27. 4±5. 9	15. 4–38. 5	13	23. 8±7. 9	10. 3–39. 1
F	50	20. 9±5. 5	11. 1–34. 6	48	21. 3±3. 7	11. 1–30. 4
30–39						
S	39	23. 3±7. 1	10. 2–37. 8	42	24. 7±6. 8	12. 8–35. 9
F	93	22. 3±5. 4	10. 8–33. 3	108	21. 8±5. 0	10. 8–33. 3
40–49						
S	74	24. 2±7. 4	11. 4–41. 9	64	23. 4±7. 0	11. 1–44. 2
F	93	21. 9±6. 1	9. 3–35. 7	120	22. 7±5. 2	9. 5–32. 6
50–59						
S	73	24. 4±6. 9	11. 9–40. 0	77	24. 2±5. 7	11. 5–40. 0
F	70	21. 0±6. 0	7. 8–36. 5	85	23. 2±6. 8	8. 5–34. 0
60–69						
S	65	24. 4±6. 9	8. 3–39. 3	75	28. 2±7. 0	13. 6–44. 1
F	38	23. 1±6. 2	10. 1–41. 2	69	25. 7±6. 0	11. 7–39. 3
70–79						
S	66	26. 2±7. 1	8. 1–39. 7	62	27. 0±8. 1	13. 5–43. 0
F	32	24. 4±5. 5	14. 7–35. 1	62	26. 3±6. 8	7. 9–40. 3
80–89						
S	58	24. 4±6. 3	8. 4–37. 6	74	28. 1±6. 6	13. 8–44. 8
F	24	25. 0±6. 3	12. 9–37. 6	47	28. 2±6. 1	10. 0–39. 0
90–99						
S	52	25. 9±6. 9	12. 6–41. 0	55	28. 2±8. 5	11. 7–48. 9
F	22	24. 7±5. 8	14. 3–36. 4	47	28. 9±7. 3	14. 3–47. 4
100–109						
S	43	26. 4±5. 7	9. 7–36. 1	39	29. 4±6. 8	16. 0–45. 7
F	5	26. 0±7. 8	18. 0–35. 6	23	30. 4±7. 3	15. 8–43. 5
110–119						
S	30	24. 4±4. 7	13. 4–30. 4	30	34. 2±9. 3	14. 8–50. 0
F	13	24. 6±4. 2	19. 8–31. 8	35	28. 5±5. 4	13. 4–39. 6
120–129						
S	16	22. 5±5. 5	9. 4–31. 4	6	28. 0±3. 9	23. 4–32. 8
F	24	23. 1±4. 0	15. 4–28. 9	18	27. 7±4. 0	20. 5–37. 2
130–139						
S	13	21. 6±5. 1	14. 1–33. 6	2	30. 2±2. 0	28. 8–31. 6
F	16	22. 7±3. 4	16. 9–28. 5	10	26. 9±4. 4	22. 3–35. 8

The variability of growth of juvenile crabs causes irregularity in the recruitment of harvestable crabs (larger than about 120 mm. wide) and in the time of crab maturity. For example, of two 21-mm.-wide males that molted seven times in salt water from May to August (in 101 days and 103 days), one attained 139 mm. and the other only 115 mm. The smaller crab would be more likely to escape the fishery to complete its life history (crabs smaller than 120 mm. made up less than 5 percent of the commercial catch). Another example is the difference in growth of two females in salt water that were 34 mm. wide in spring. One matured after four molts and 78 days (114 mm.); the other after seven molts and 179 days (175 mm.). The individual maturing at 114 mm. did not attain harvestable size and probably would have spawned in summer. The 175-mm. female was acceptable for market during its last two instars and had it escaped the fishery it probably would have spawned in fall.

WINTER

Blue crabs grow during the winter in the St. Johns River but more slowly than in summer. I observed 287 molts among crabs in salt water (November 20, 1964, to March 31, 1965) and 258 in fresh water (November 22, 1965, to March 31, 1966).

Water temperatures in winter averaged 11.8° C. lower in salt water and 13.5° C. lower in fresh

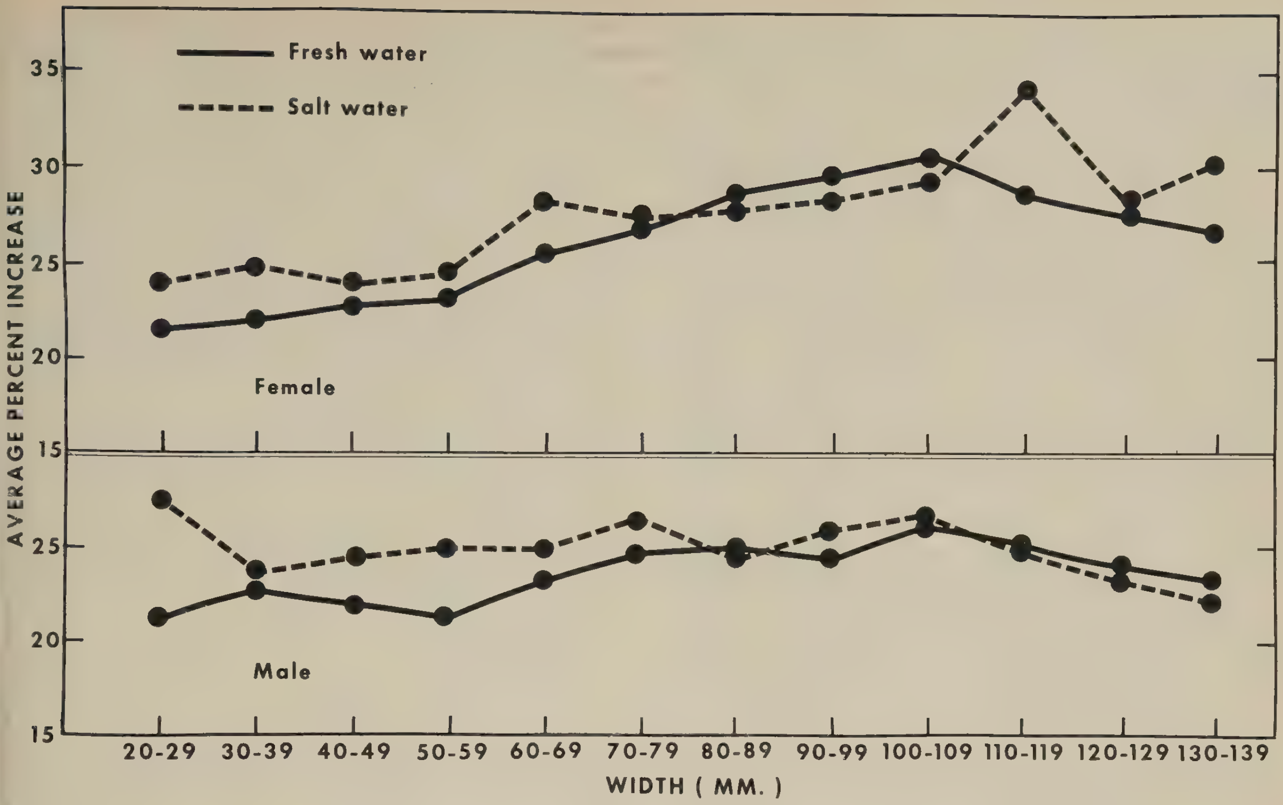

FIGURE 2.—Relative growth per molt of female and male blue crabs in fresh and salt water, St. Johns River, Fla., April 1 to November 15, 1964 and 1965.

water than in summer; salinities at the salt water station were 4.3 p.p.t. lower. Mean water temperature was 15° C. in salt water (range, 8.3°–22.9° C.) and 12.3° C. in fresh water (range, 3.8°–18.2° C.). Salinity at the Cedar Point Creek site averaged 14.5 p.p.t. (range, 6–23.3 p.p.t.).

Relative growth per molt in winter was similar to that in summer. Crabs were less active and consumed less food but generally were in good condition.

MOLT INTERVAL

Information was collected on molting in summer and winter.

SUMMER

More than one-half (1,256) of the molts in summer (April 1 to November 15) from crabs that molted more than once provided information on molt interval.

Molt intervals appeared to be affected by the size of crabs and by season but not by sex and salinity. I found little difference in molt interval between males and females or between salt and fresh water. The time between molts increased with increasing body size (table 3). The smallest crabs (20–29 mm. wide) molted after an average of 11 days, and those over 120 mm. wide after an average of 42 days. Molt intervals of crabs within each size group varied greatly but usually were shortest during the warmest months, June to September. Most juveniles 30 to 39 mm. wide in April reached harvestable size after 4 months, but crabs that had the same width in June were harvestable after 3 months with the same number of molts. Crabs that molted after particularly long periods grew little or died.

Information was obtained on the time needed for the terminal molt of 101 female blue crabs (83–139 mm. wide). The final molt interval for 85 percent of these crabs ranged from 25 to 50 days. Two females molted in as few as 18 days. Large crabs (above 110 mm. wide) averaged 5 days longer than smaller ones. In salt water (crabs averaged 106 mm. wide), the mean interval

Table 3.—*Molt interval in the blue crab, by 10-mm.-width groups, St. Johns River, Fla., April 1 to November 15, 1964 and 1965*

[Salt- and fresh-water data combined; ranges in parentheses]

Width group	Crabs		Mean molt interval, standard deviation, and range	
	Male	Female	Male	Female
Mm.	*Number*	*Number*	*Days*	*Days*
20–29	23	18	12±5.0 (7–25)	10±2.4 (7–17)
30–39	61	77	15±4.6 (7-34)	13±3.8 (6–27)
40–49	100	101	17±6.1 (8–38)	18±6.1 (9–42)
50–59	101	99	21±7.9 (9–51)	20±9.0 (9–49)
60–69	67	87	23±9.2 (11–54)	21±10.3 (9–68)
70–79	69	51	22±8.5 (11–64)	24±9.5 (11–59)
80–89	46	65	28±10.5 (16–68)	26±11.5 (14–77)
90–99	52	47	31±9.1 (20–64)	30±8.8 (17–60)
100–109	36	39	32±9.2 (21–65)	33±7.2 (20–52)
110–119	29	38	34±7.8 (19–53)	39±10.2 (18–61)
120–129	17	15	43±12.0 (22–68)	43±8.4 (26–59)
130–139	13	5	41±9.6 (27–56)	41±7.4 (35–54)

before the final molt was 38 days (range, 18–77 days); in fresh water (crabs averaged 117 mm.), it was 40 days (range, 18–61 days).

WINTER

Data on molt intervals (from animals that molted more than once in confinement) were obtained on 112 crabs in salt water and 96 in fresh water during winter (November 20 to March 31). The time between molts was three to four times as long in winter as in the rest of the year. The mean interval was 46 days for crabs 20 to 29 mm. wide and rose to 124 days for an individual 92 mm. wide (table 4). Most juveniles 20 to 59 mm. wide molted two or three times, but many of those larger than 99 mm. did not molt (table 5).

Table 4.—*Molt interval in the blue crab, by 10-mm.-width groups, St. Johns River, Fla., November 20 to March 31, 1964–65 and 1965–66*

[Salt- and fresh-water data combined]

Width group [1]	Crabs	Molt interval	
		Mean and standard deviation	Range
Mm.	*Number*	*Days*	*Days*
20–29	16	46±25.8	21–96
30–39	48	47±15.8	20–100
40–49	49	59±17.8	22–94
50–59	35	72±17.3	28–101
60–69	37	79±18.1	46–118
70–79	18	91±19.4	69–123
80–89	4	106±17.0	81–120
90–99	1	124	--------

[1] Crabs wider than 99 mm. did not molt more than once.

Temperature has a major influence on the molt interval. In Chesapeake Bay, growth of blue crabs usually ceases during the colder months from November to early April (Van Engel, 1958). In the St. Johns River, low temperatures delay but do not prevent molting. I observed crabs shedding their old shells at water temperatures as low as 3.8° C. Molting in winter was less frequent at the lower water temperatures. The numbers of molts were about the same in November and March (mean water temperature 16° C.) as during the 3 months, December–February (mean water temperature 12.5° C.). Extended observations in fresh water indicated that almost all of the crabs that did not grow in winter molted during the first 3 weeks of April (mean water temperature had risen to 18.2° C.).

ESTIMATE OF ABSOLUTE GROWTH

Mean percentage growth per molt (25.3) and mean molt interval per size group (for summer and winter) were used with relevant data from laboratory experiments on blue crabs less than 20 mm. to obtain gross estimates of increase in body size with age. Although the floats would not hold crabs smaller than 20 mm. wide, I have data on two individuals that reached this size when hatched and reared in the laboratory. After metamorphosis to the first crab stage, one of these crabs went through 10 molts in 68 days to reach 23 mm.; the other took nine molts and

Table 5.—*Frequency of molting of blue crabs, by 10-mm.-width groups, St. Johns River, Fla., November 20 to March 31, 1964–65 and 1965–66*

[Salt- and fresh-water data combined; no crabs molted more than three times]

Width group	Crabs	1 molt	2 molts	3 molts
Mm.	*Number* [1]	*Number*	*Number*	*Number*
20–29	40	40	39	22
30–39	43	43	40	14
40–49	58	58	46	2
50–59	46	46	33	0
60–69	37	37	10	0
70–79	31	31	1	0
80–89	41	40	0	0
90–99	24	19	0	0
100-109	12	7	0	0
110-119	25	14	0	0
120–129	27	3	0	0
130–139	6	0	0	0

[1] Not included are 10 crabs that died before molting once. Deaths after one molt: 1(20–29), 1(30–39), 1(40–49), and 1(60–69); after two molts, 1(40–49).

69 days to reach 20 mm. The mean percentage growth per molt was the same as in larger crabs. To estimate the time needed to attain harvestable size, I used 25.3 percent to calculate relative increases from the 1st crab stage (2.5 mm.) to a 19th crab stage (142 mm.), applied mean molt intervals, and allowed 1½ months for larval development (Costlow and Bookhout, 1959). These calculations indicate that most blue crabs in the St. Johns River reach harvestable size within 1 year after hatching (table 6).

Table 6.—*Estimated growth by month of St. Johns River, Fla., blue crabs hatched in April, July, and October*

Month	Maximum width		
	Mm.	*Mm.*	*Mm.*
April	[1] 1	----------	----------
May	5	----------	----------
June	12	----------	----------
July	23	[1] 1	----------
August	46	5	----------
September	58	12	----------
October	90	23	[1] 1
November	113	46	5
December	113	46	8
January	113	58	10
February	113	58	12
March	142	72	15
April	----------	90	29
May	----------	113	46
June	----------	142	72
July	----------	----------	90
August	----------	----------	113
September	----------	----------	142

[1] Larvae.

MORTALITY OF EXPERIMENTAL ANIMALS

I recorded deaths of 94 blue crabs in salt water and 212 in fresh water during the summer. Mortality was 8 percent for crabs 20 to 79 mm. wide and 19 percent for those 80 to 139 mm. Most crabs that died were well past the average molt interval of their size group.

Only eight animals died in salt water (two after molting once) and seven in fresh water (three after molting once) during the winter—a mortality of 3 percent.

Year-round mortality at ecdysis was 36 crabs (salt water, 11; fresh water, 25) out of a total of 2,782 molts. The few deaths at ecdysis indicate that molting in itself may not be a critical source of mortality. In nature, however, crabs are easy prey immediately after they emerge from their shells.

SUMMARY

From April 1964 through March 1966, juvenile blue crabs (20–139 mm. wide) were held in floats in St. Johns River to determine growth increments, molt intervals, and the effects of salinity and temperature on growth.

Measurements of 2,000 blue crabs, 10 to 149 mm. wide, collected in the river indicated that the length-width ratio decreased as the animals grew. This decrease was less among males than females.

In salt water (salinity greater than 5 p.p.t.), data were obtained on 1,085 molts during the summer (April 1 to November 15) and on 287 during the winter (November 20 to March 31); in fresh water—on 1,152 molts in summer and 258 in winter.

Growth increments per molt varied from 7.8 to 50 percent in summer, and mean increment, by 10-mm.-width groups, was 20.9 to 34.2 percent. Among larger crabs, females usually had greater width increments than males. Percentage growth in the terminal molt of females averaged 34.4 in salt water and 30.2 in fresh water. Males and females showed significant difference in growth between fresh and salt water. Each sex generally averaged the most growth per molt in salt water.

Relative growth per molt in winter was similar to that in summer.

Molt intervals in the summer did not appear to be affected by the sex of the crab and the salinity of the water, but were affected by crab size and water temperature. The smallest crabs (20–29 mm. wide) molted after an average of 11 days and animals over 120 mm. wide after an average of 42 days. Molt intervals usually were shortest during the warmest months. The interval of the terminal molt of females averaged 38 days in salt water (mean width, 106 mm.) and 40 days in fresh water (mean width, 117 mm.).

The time between molts was three to four times as long in winter as in summer. Most juveniles 20–59 mm. wide molted two or three times, but many of those larger than 99 mm. did not molt.

Calculations based on the data presented indicate that most blue crabs in the St. Johns River reach harvestable size within 1 year after hatching.

Year-round mortality at ecdysis at both sites was only 36 crabs out of a total of 2,782 molts; other deaths totaled 285.

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DISTRIBUTION OF BROWN SHRIMP (*Penaeus aztecus aztecus* IVES) AS RELATED TO TURBID WATER PHOTOGRAPHED FROM SPACE[1]

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ABSTRACT

Visual evidence of probable relief currents in the northwestern Gulf of Mexico is provided for the first time by photographs taken from Gemini spacecraft. After rectification of photographs of the Continental Shelf off the Texas Coast, a comparison of the position of relief currents to areas of high shrimp production indicates that photography from space can be a valuable tool for fishery research.

Oceanographers long have predicted the existence of relief or rip currents between Galveston and Corpus Christi, Tex. (Sweitzer, 1898; Smith, Medina, and Abella, 1951; Curray, 1960), and navigators have called the area the "Whirlpool of the Gulf" (U.S. Coast and Geodetic Survey, 1949). The offshore relief currents result from the convergence of southerly and northerly currents, which causes a piling up of water that is relieved by an offshore flow. The buildup and eventual release of waters in the Galveston-Corpus Christi area are continuously recurring sequences of events related to the total Gulf system.

Visual evidence of countercurrents, which have never before been documented by oceanographic techniques, is apparently provided by figure 1. This figure is a reproduction of a color photograph taken by NASA (National Aeronautics and Space Administration) from an altitude of 330 km. on November 14, 1966. In addition to showing the distribution of suspended material in bay and Gulf waters, the discharge patterns from the bays, the major eddy currents, and the relative direction of the currents, we believe it illustrates clearly the long-suspected phenomenon of rip or relief currents.

Sediments in the water provide the contrast that permits us to see the interaction of the coastal current systems. Perhaps the most obvious feature is the discharge of sediment at the entrances to Lake Charles, La., and Sabine Lake and Galveston Bay, Tex. Large volumes of sediment in these areas are being carried into the Gulf and immediately transported southward by an alongshore current. Less noticeable but vastly larger are two areas of discolored water south of Galveston that extend eastward. These plumes of suspended material are aligned by moving water and most likely represent the areas of rip or relief currents predicted by oceanographers. The plumes, outlined in figure 2, are believed to be semipermanent features of the Gulf current system, although their locations, intensity, and dimensions undoubtedly fluctuate throughout the year. Obviously, they must have some effect on the bottom sediments and nutrient supply.

Our conclusions admittedly are conjectural because of the lack of necessary detailed physical and chemical data from oceanographic and bottom surveys made in and around the areas under consideration. A definite relation does exist, however, between the shrimp catch, trawling frequency, and the plumes shown in figure 2.

Rectification of the Gemini photograph to ONC (Operational Navigation Chart) No. 24 (fig. 3) revealed that the plumes were in BCF (Bureau of Commercial Fisheries) statistical area 19 and the lower portion of area 18 (fig. 4). The best

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[1] Contribution No. 276, Bureau of Commercial Fisheries Biological Laboratory, Galveston, Tex. 77550.

[2] Present address: TRW Systems, 1 Space Park, Redondo Beach, Calif. 90278.

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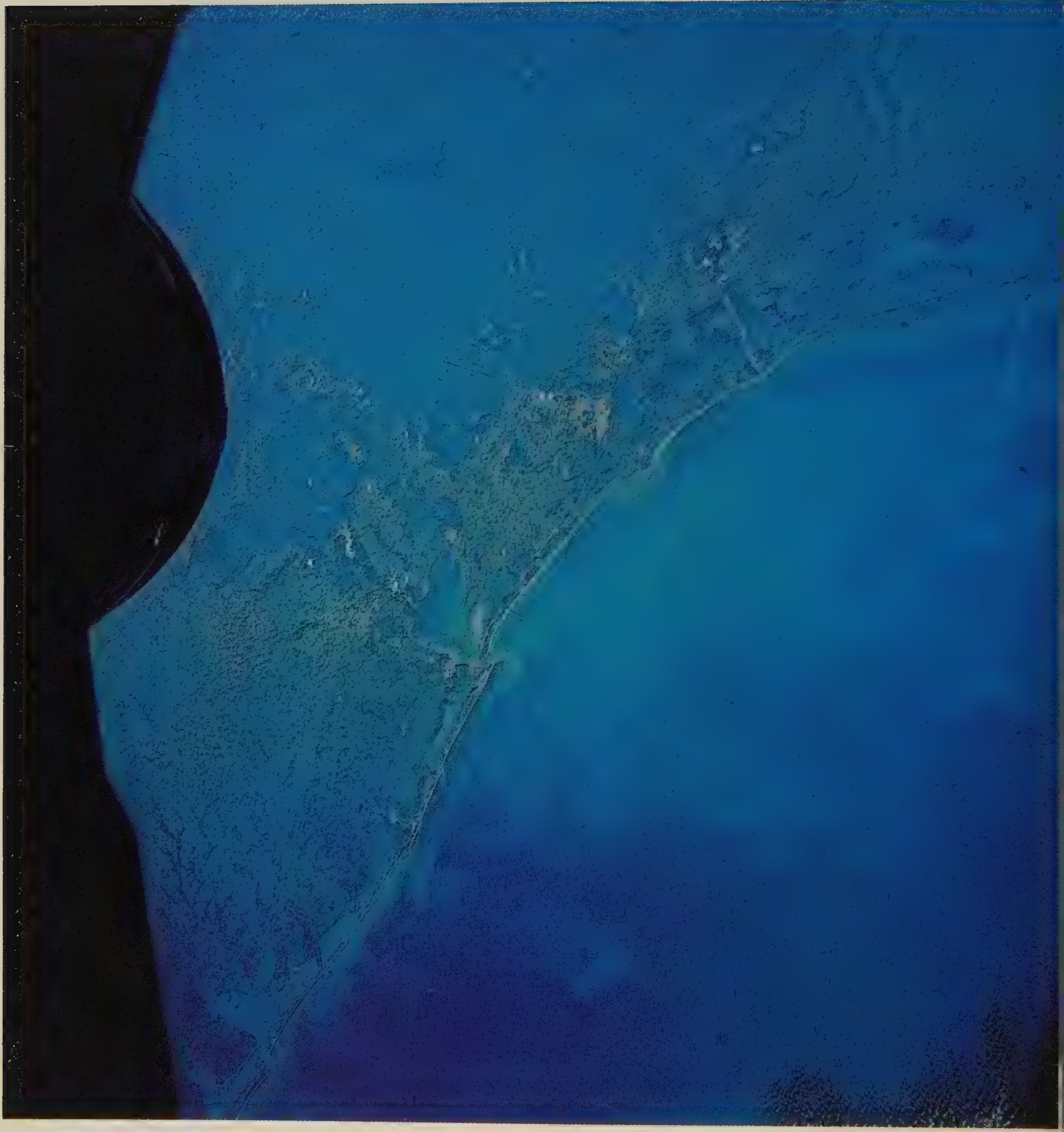
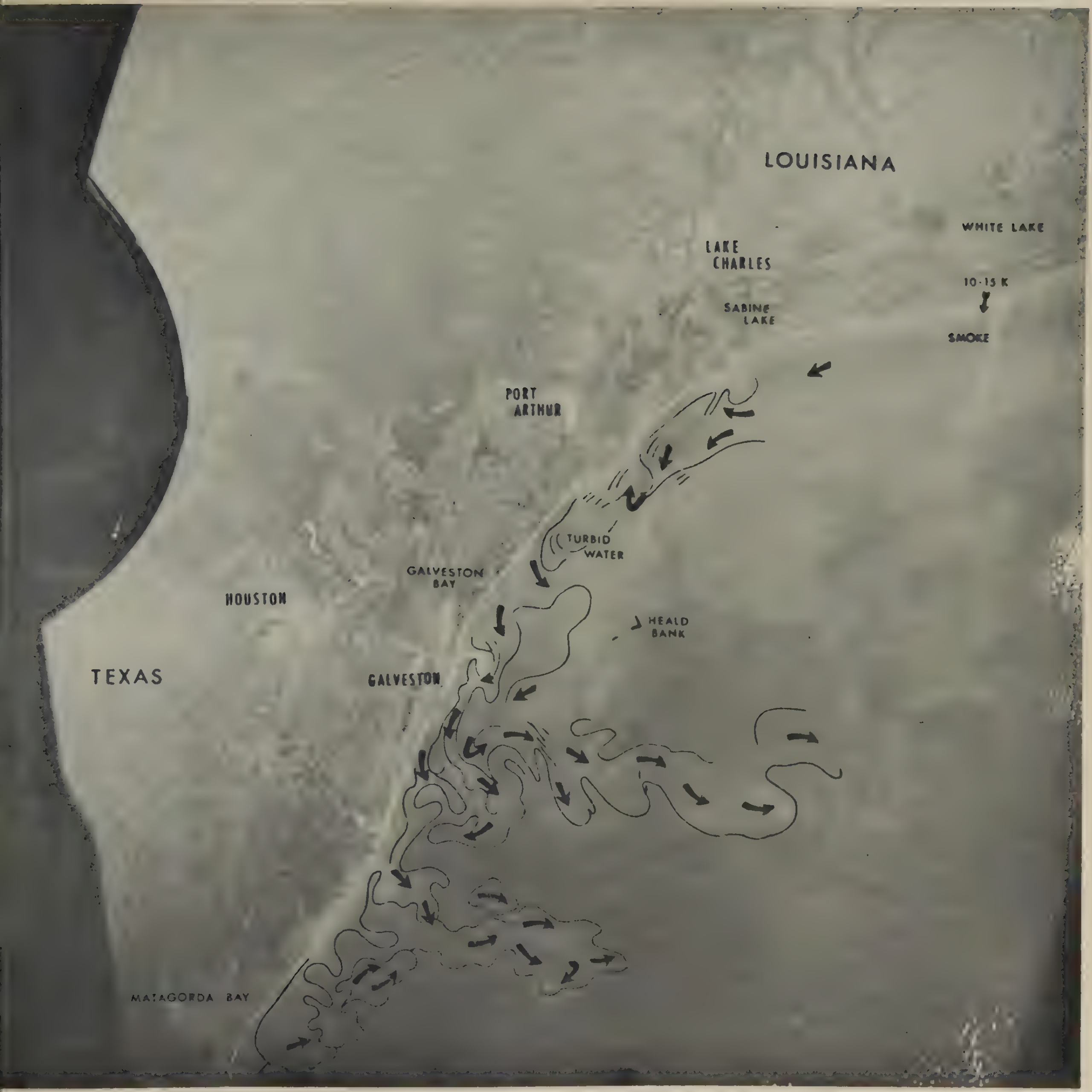


FIGURE 1.—An unrectified Gemini photograph of the northwestern Gulf of Mexico, from an altitude of 330 km. Matagord Bay, Tex., is to the lower left and White Lake, La., to the upper right. The direction of the wind can be determine from the smoke trailing offshore near White Lake. The discharge patterns from the bays and the southerly along shore currents are plainly visible. What appear to be offshore relief currents are evident south and east of Galveston Tex. The white dots along the right margin are clouds; a portion of the Gemini craft is on the left margin. (NAS color photograph S–66–63034, taken by James A. Lovell, Jr., and Edwin E. Aldrin, Jr., November 14, 1966 (130 hours local time), during Gemini Flight XII).


LOUISIANA
WHITE LAKE
LAKE CHARLES
10-15 K
SABINE LAKE
SMOKE
PORT ARTHUR
TURBID WATER
GALVESTON BAY
HOUSTON
HEALD BANK
TEXAS
GALVESTON
MATAGORDA BAY

IGURE 2.—This reproduction of figure 1 shows the alongshore southerly currents and what we believe to be the offshore relief or rip currents south and east of Galveston, Tex.

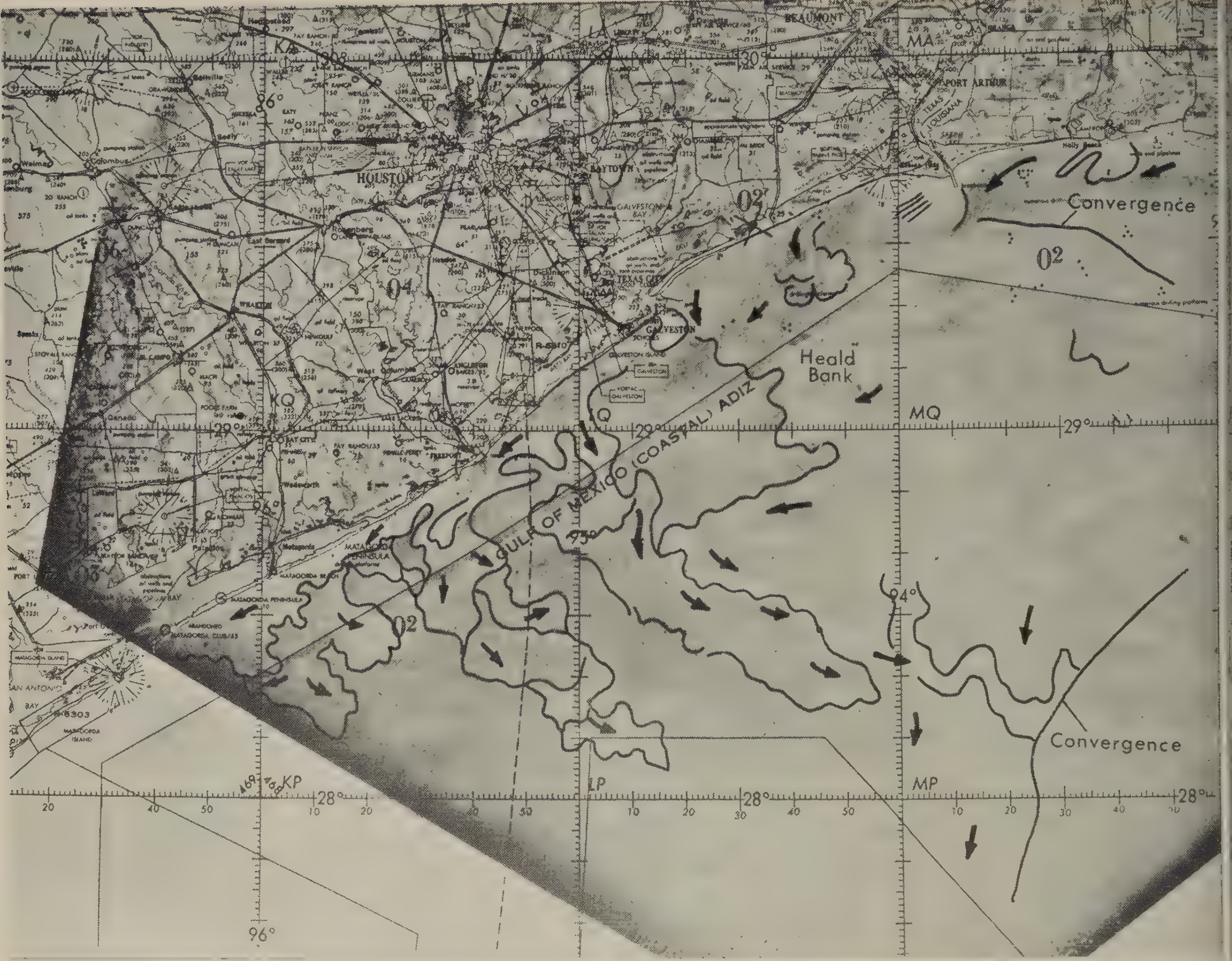


FIGURE 3.—An image of *ONC No. 24*, superimposed over a portion of figure 1 (rectified). The plumes have been outlined, and the directions of the currents are shown by arrows.

fishing grounds for brown shrimp (*Penaeus aztecus aztecus* Ives) in the northern Gulf of Mexico are known to be consistently in this region. In November 1966 (when the Gemini photograph was taken) about 57 percent of the catch of brown shrimp along the Texas Coast came from statistical area 19 and about 54 percent of the fishing effort was expended in this area (table 1). In 1956–66 about 43 percent of the brown shrimp caught in Gulf waters along the Texas Coast came from statistical area 19 (table 2).

TABLE 1.—*Catch and fishing effort for brown shrimp, by statistical areas, in the Gulf of Mexico along the Texas Coast, November 1966* [1]

Statistical area	Catch		Effort (trips)	
	Metric tons	*Percent*	*Number*	*Percent*
18	36.7	4.6	119	9.5
19	450.4	56.9	684	54.4
20	99.4	12.6	166	13.2
21	205.5	25.9	288	22.9
Total	792.0	100.0	1,257	100.0

[1] Source: Gulf Coast shrimp data, reported by depth and area of capture, species, size, number of trips, and days fished, November 1966. U.S. Fish Wildl. Serv., Curr. Fish. Statist. 4358.

Additional evidence for the relation between the plumes and brown shrimp fishing is provided by data gathered in July–September 1964 by personnel of the BCF Biological Laboratory, Galveston, Tex. During this period, which is the height of the brown shrimp season, an extensive interview campaign was undertaken to determine, by 10-minute grids, the areas most frequented by vessels fishing for brown shrimp. These data have been

TABLE 2.—*Catch of brown shrimp (heads-off), by statistical areas, in the Gulf of Mexico along the Texas Coast* [1]

Year	Statistical area				
	18	19	20	21	Total
	Thousands of metric tons				
956	2.2	3.1	3.3	1.4	10.0
957	2.4	5.3	3.4	1.6	12.7
958	2.2	2.8	4.6	1.3	10.8
959	2.3	4.9	3.6	2.5	13.4
960	3.4	7.0	2.9	1.7	15.0
961	1.1	2.5	2.1	1.3	7.0
962	1.0	3.4	2.4	.8	7.6
963	1.6	6.1	2.0	1.8	11.5
964	1.2	4.0	2.4	1.0	8.6
965	1.9	6.4	1.9	1.6	11.8
966	1.3	5.7	2.6	2.0	11.6
Total	20.6	51.2	31.2	17.0	120.0
ercentage	17.1	42.7	26.0	14.2	100.0

[1] Source: Published records of the U.S. Department of the Interior, Bureau f Commercial Fisheries.

uperimposed on the rectified Gemini photograph n figure 5. Clearly, fishing intensity was heaviest n and near the plumes.

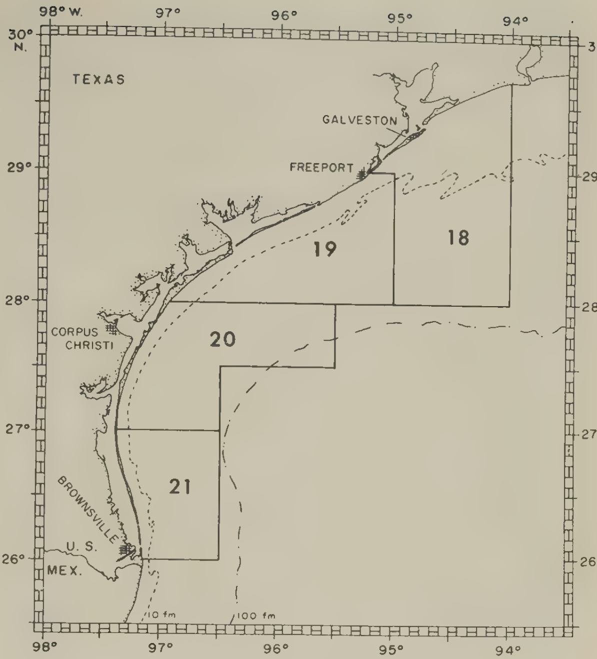


FIGURE 4.—Statistical areas along the Texas Coast. By interviewing fishermen, BCF employees are able to record data on daily landings and fishing effort by statistical area. The recording of catch and effort by this method began in January 1956. Comparison of this figure with figure 3 shows that the relief plumes lie in statistical area 19 and the lower portion of 18.

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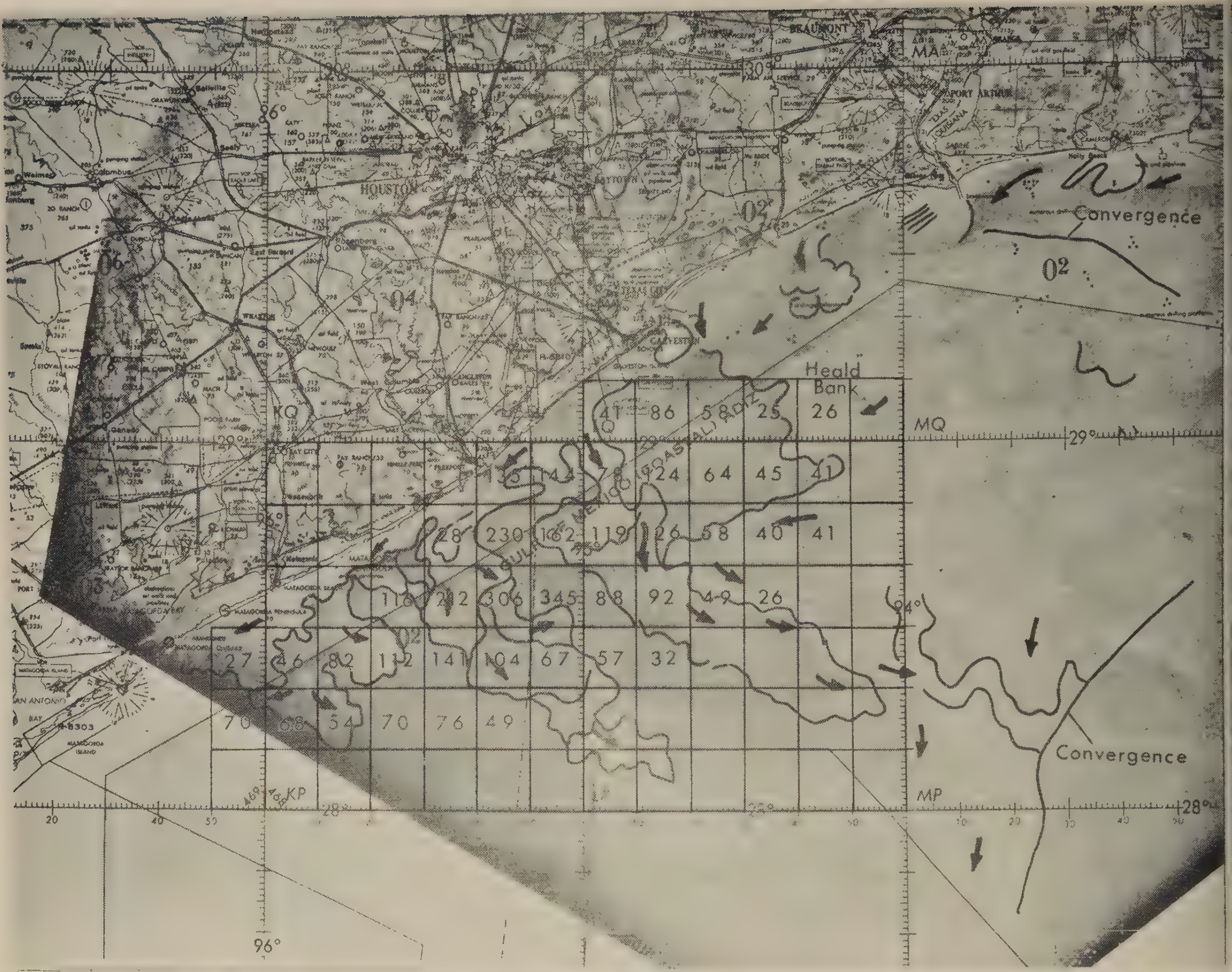
HOUSTON
BEAUMONT
PORT ARTHUR
GALVESTON
Convergence
02
Heald Bank
41
86
58
25
26
MQ
29°
78
124
64
45
41
28
230
162
119
26
58
40
41
116
212
306
345
88
92
49
26
27
46
82
112
141
104
67
57
32
70
68
54
70
76
49
94°
Convergence
KQ
KP
MP
28°
96°

FIGURE 5.—An overlay on figure 3 that demonstrates the relation between the plumes and fishing intensity for brown shrimp. The numbers in the 10-minute grids represent the total number of vessels fishing in each grid in July–September 1964. Only those grids are numbered where 25 or more vessels fished.

PHYSICAL AND CHEMICAL LIMNOLOGY OF BROWNLEE RESERVOIR, 1962–64

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Seattle, Washington 98102

ABSTRACT

The physical and chemical features of Brownlee Reservoir are discussed in relation to seasonal change, inflow and outflow, operation of the dam, modified environment of river below the dam, and possible effects of these factors on behavior, passage, and survival of salmon (*Oncorhynchus* spp.).

Temperature, oxygen concentration, and current were the most critical factors affecting the distribution and survival of salmon. Water temperature above 26.7° C. and oxygen concentration below 3 p.p.m. limited the area of suitable habitat during midsummer; environmental conditions in the spring, fall, and winter were suitable, if not optimal. The reservoir had a significant effect on the temperature and oxygen concentrations of the Snake River below the dam. In October, discharge from the reservoir was 5° C. warmer than the water entering the reservoir; oxygen concentration was 5 p.p.m. lower than in the inflow. This condition reversed in June and July.

Current velocities and directions changed significantly with changes in river inflow, discharge rate, and surface level of the reservoir. Passage by juvenile salmonids through the reservoir was affected by changes in reservoir temperature, length, oxygen concentrations, and velocity and direction of the current.

The U.S. Department of the Interior began intensive research in 1961 to solve problems of fish passage at high dams. Primary consideration was given to the study of factors that might affect the survival and passage of adult and juvenile salmonids (*Oncorhynchus* spp.) under the conditions anticipated for the Middle Snake River Basin. Brownlee Reservoir, completed in 1958, provided an area in which to examine the effects of a large impoundment on migrating salmon. The Bureau of Commercial Fisheries began limnological studies (physical and chemical) in July 1962 and continued them through October 1964; the study on the effects of various environmental factors on the behavior and passage of salmonids was directed principally toward water quality and current.

Brownlee Reservoir lies at the head of the Snake River canyon in hilly and semiarid, open-range country between the borders of northeastern Oregon and midwestern Idaho (fig. 1). At full pool, the reservoir begins about 16 km. downstream from Weiser, Idaho, and continues northerly in a nearly straight course for 92 km. to Brownlee Dam. Average width is less than 0.8 km.; maximum depth at full pool is about 92 m. At full capacity, the reservoir has an area of 6,100 hectares and contains 217,000 hectare-meters, or 1.8×10^9 m.^{3} of water.

Three main tributaries—the Snake, Powder, and Burnt Rivers—and many small, intermittent streams enter the reservoir. The upper 23 km. above the mouth of Burnt River is relatively shallow and essentially a river. Depth increases sharply below Burnt River; currents in the remaining 69 km. are weak when the reservoir is at full pool. The slope of the reservoir's basin, its depth, geographic location, and especially its thermal characteristics, are such that it fits some of the criteria used by Welch (1952) and Hutchinson (1957) to describe "temperate lakes of the second order."

An obvious difference between a reservoir such

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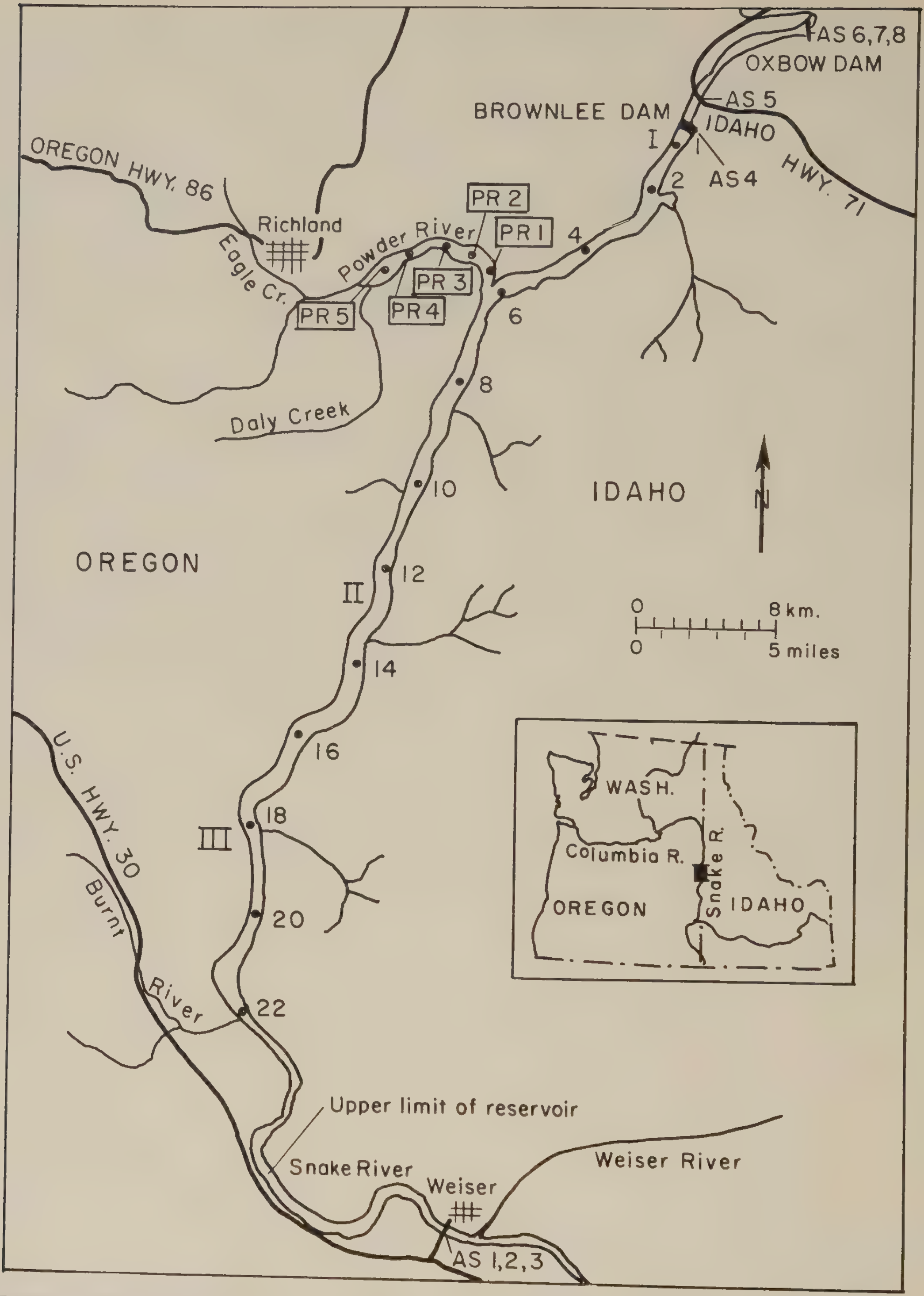
AS 6,7,8
OXBOW DAM
AS 5
BROWNLEE DAM
IDAHO
I
2
AS 4
HWY. 71
OREGON HWY. 86
Richland
Eagle Cr.
Powder River
PR 2
PR 1
4
PR 3
PR 4
PR 5
6
8
Daly Creek
10
IDAHO
N
OREGON
12
II
0
8 km.
0
5 miles
14
16
U.S. HWY. 30
18
III
WASH.
Columbia R.
Snake R.
OREGON
IDAHO
Burnt
20
River
22
Upper limit of reservoir
Weiser River
Snake River
Weiser
AS 1,2,3

FIGURE 1.—Brownlee Reservoir, showing principal limnological sampling stations. The twelve Arabic numerals without a letter prefix were the main sampling stations; Roman numerals indicate location of continuous current recorders. Stations PR 1–5 were frequently sampled stations in the Powder River and AS 1–8 were frequently sampled stations located upstream and downstream from Brownlee Reservoir.

as Brownlee and a natural river-lake system is the depth at which the water is discharged. Flows from a reservoir are usually discharged at depth, whereas flows from a lake are discharged from the surface. At Brownlee, the turbine intake is 36.6 m. below normal pool level. The spillway discharges from the surface and from a depth of 35.4 m. Fluctuation in water level is considerable during late fall and winter; the reservoir is lowered as much as 32.8 m., depending on forecasts of expected spring runoff. The fluctuations lead to terraced mudbanks that are unproductive areas. Average volumes of water from the Snake River at Weiser, Idaho, range from 255 c.m.s. (cubic meters per second) in late summer to 1,132 c.m.s. in the spring. Maximum rate of flow during the study period was about 1,416 c.m.s.[1]

METHODS

Sampling stations were established throughout Brownlee Reservoir and at certain locations upstream and downstream from the reservoir to measure physical and chemical properties of its water. Temperature, dissolved oxygen concentration, and current were the principal factors studied. The location of sampling stations and the techniques and equipment used are described.

SAMPLING LOCATIONS AND TECHNIQUES

We established sampling stations throughout the reservoir and at certain locations upstream and downstream from it (fig. 1). Twelve main stations were spaced about 6 km. apart on the axis of the reservoir. They extended from 1 to 69 km. above the dam. Occasional sampling was done between these main stations. Additional stations along the Snake River included sites on State highway 30 at the bridge in Weiser, State highway 71 on interstate bridge below Brownlee Dam, and on the catwalk below the Oxbow and Brownlee power plants. Other stations were at Eagle Creek (on the Powder River) and at five places in the Powder River arm of Brownlee Reservoir. Water samples were also collected at fish-trapping sites throughout the reservoir during the periods of migration by salmon.

All permanent stations were sampled once every 2 weeks during summer stratification of the water in 1962 and once a month in winter and early spring after turnover of the water in 1963–64. Permanent stations were marked by Styrofoam[2] buoys anchored to concrete blocks to assure sampling at the same location each period.

Four sets of diurnal observations were made in addition to the routine sampling. These observations covered either a 24- or 48-hour period; samples were taken every 3 to 6 hours.

To secure temperature profiles from top to bottom and define the epilimnion, thermocline, and hypolimnion when present, depth and conductivity readings were recorded with each temperature change of 0.55° C. as read from a Whitney thermistor and conductivity meter. The thermistor was calibrated daily with a certified laboratory thermometer and checked periodically at various depths with a mercury reversing thermometer. The conductivity meter was calibrated daily.

During periods of stratification, water samples were taken in 2½-liter plastic Van Dorn bottles to determine dissolved oxygen and other characteristics in each of the three water masses. Before and after stratification, sampling was from the surface to the bottom at intervals up to 15 m. Samples were kept in an insulated cooler to minimize chemical changes that might be caused by increasing temperature. Dissolved oxygen was determined by the unmodified Winkler method (American Public Health Association, 1960); a second subsample was drawn and placed in a plastic bottle for later determination of free carbon dioxide, sulphate, turbidity, total and phenolphthalein alkalinity, and pH. Duplicate samples from some of the same casts were collected at least once every sampling day to check accuracy of all determinations.

Daily maximum and minimum air temperatures, precipitation, and wind direction and velocity were recorded at two stations. Meteorological data were received from the weather station operated by Radio Station KWEI at Weiser, Idaho. A second weather station was established near station 14 on the west side of the reservoir.

A temperature profile was determined by taking the temperature from top to bottom and recording the depth at every temperature change of 1° F.

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[1] A flow of 2,209 c.m.s. was recorded in December 1964 (after the study ended).

[2] Trade names referred to in this publication do not imply endorsement of commercial products by the Bureau of Commercial Fisheries.

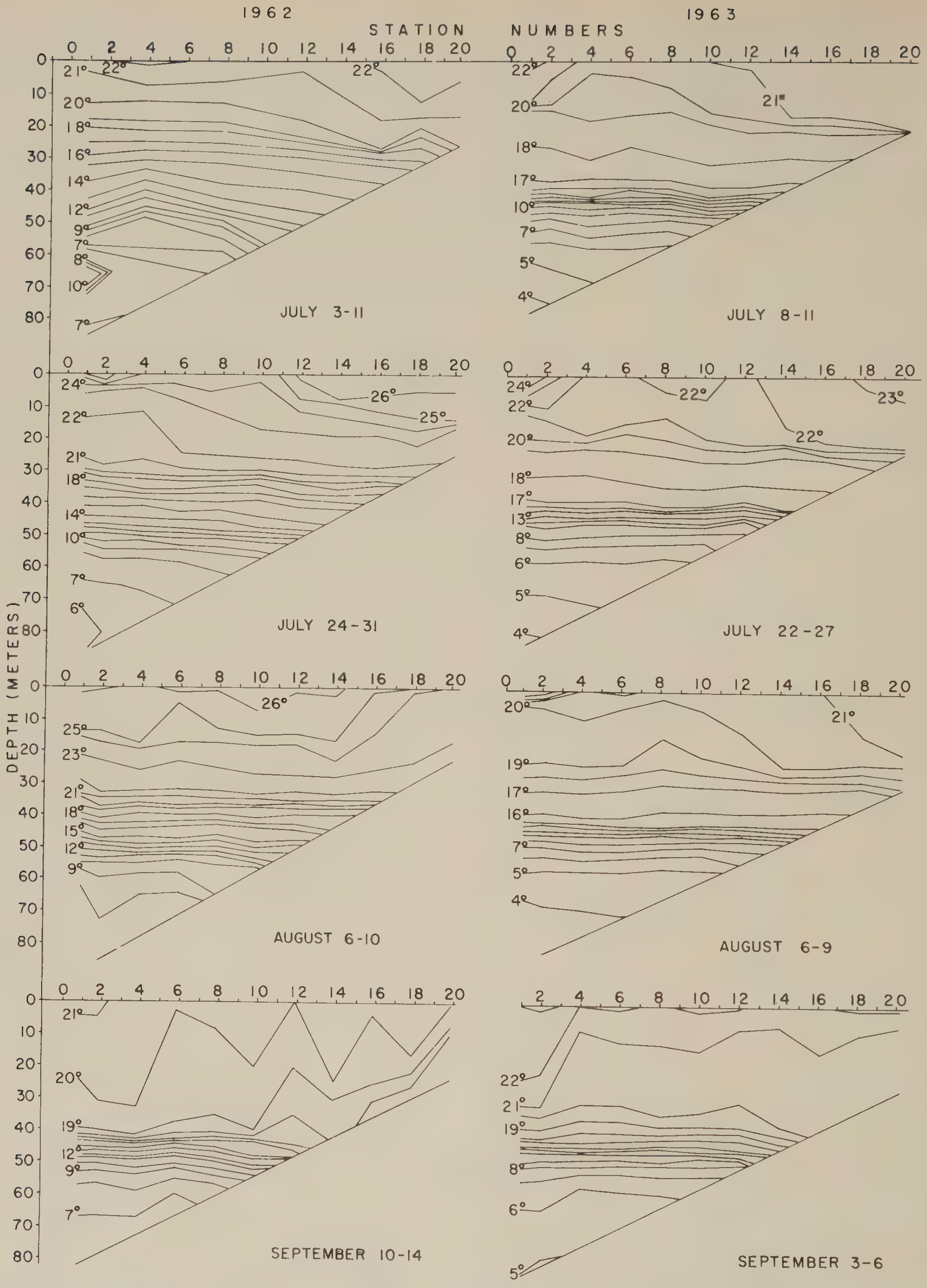


Figure 2.—Temperature profiles (° C.), Brownlee Reservoir. Comparison of months, July 1962 to June 1964.

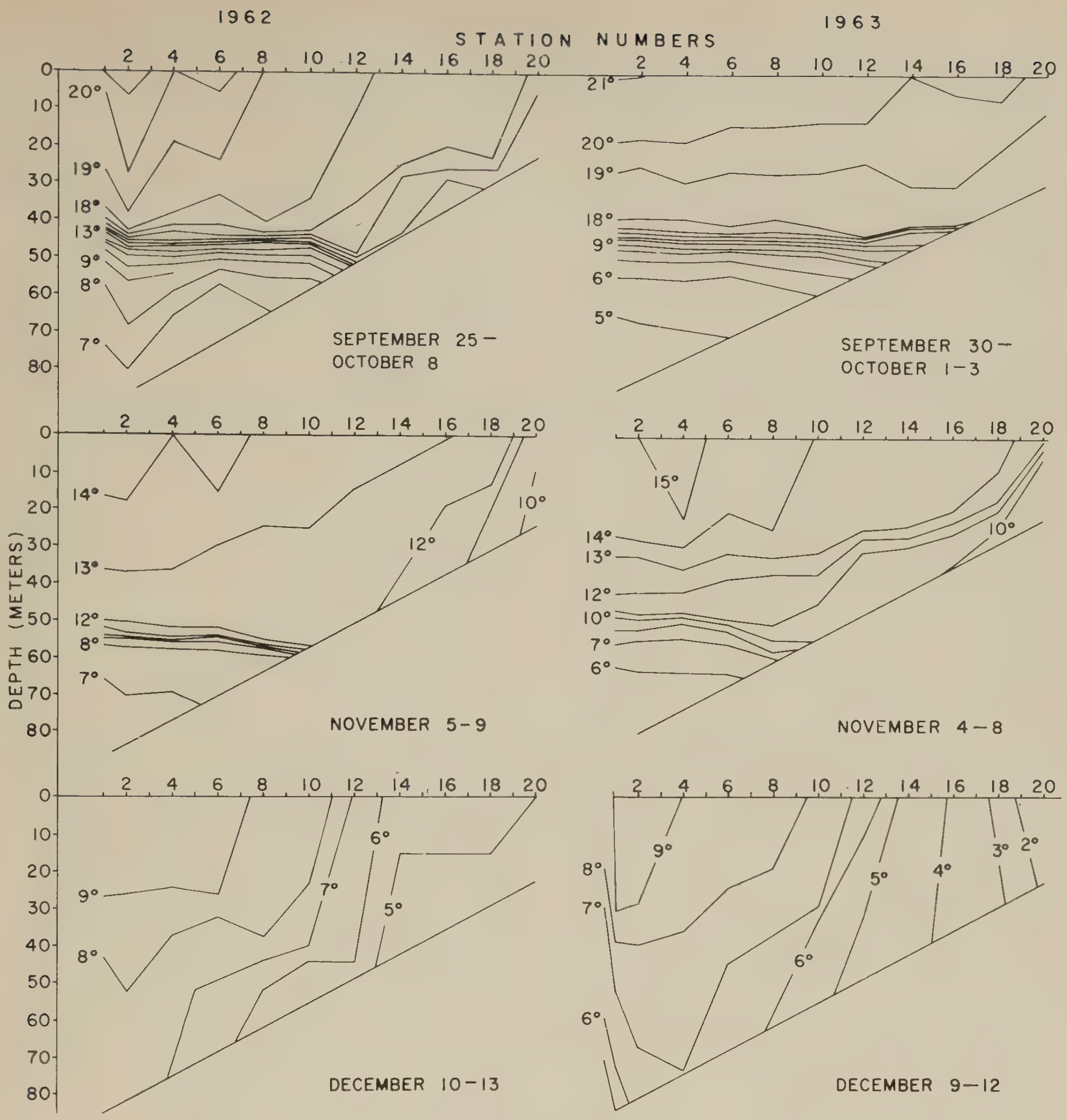


FIGURE 2.—Continued

0.55° C.). Conductivity readings were also reorded at each change of 1° F. Temperature data ere then graphed to determine the depths of the pilimnion, thermocline, and hypolimnion.

Along with Secchi disc readings, air temperaure, wind velocity and direction, other atmosheric conditions also were recorded routinely at ach station.

Mean volumes of flow from the Snake River into he reservoir and discharges from Brownlee Resrvoir were computed during each sampling period. Mean temperatures of the inflow and outflow volumes were also computed for each period from thermograph, Whitney thermistor, and laboratory thermometer records. Table 1 summarizes temperature and inflow-outflow computations.

CURRENT MEASUREMENTS

Measurement of current velocity and direction with three Savonius-type current meters began in the fall of 1963. The meters were used as continuous current recorders at a given depth and loca-

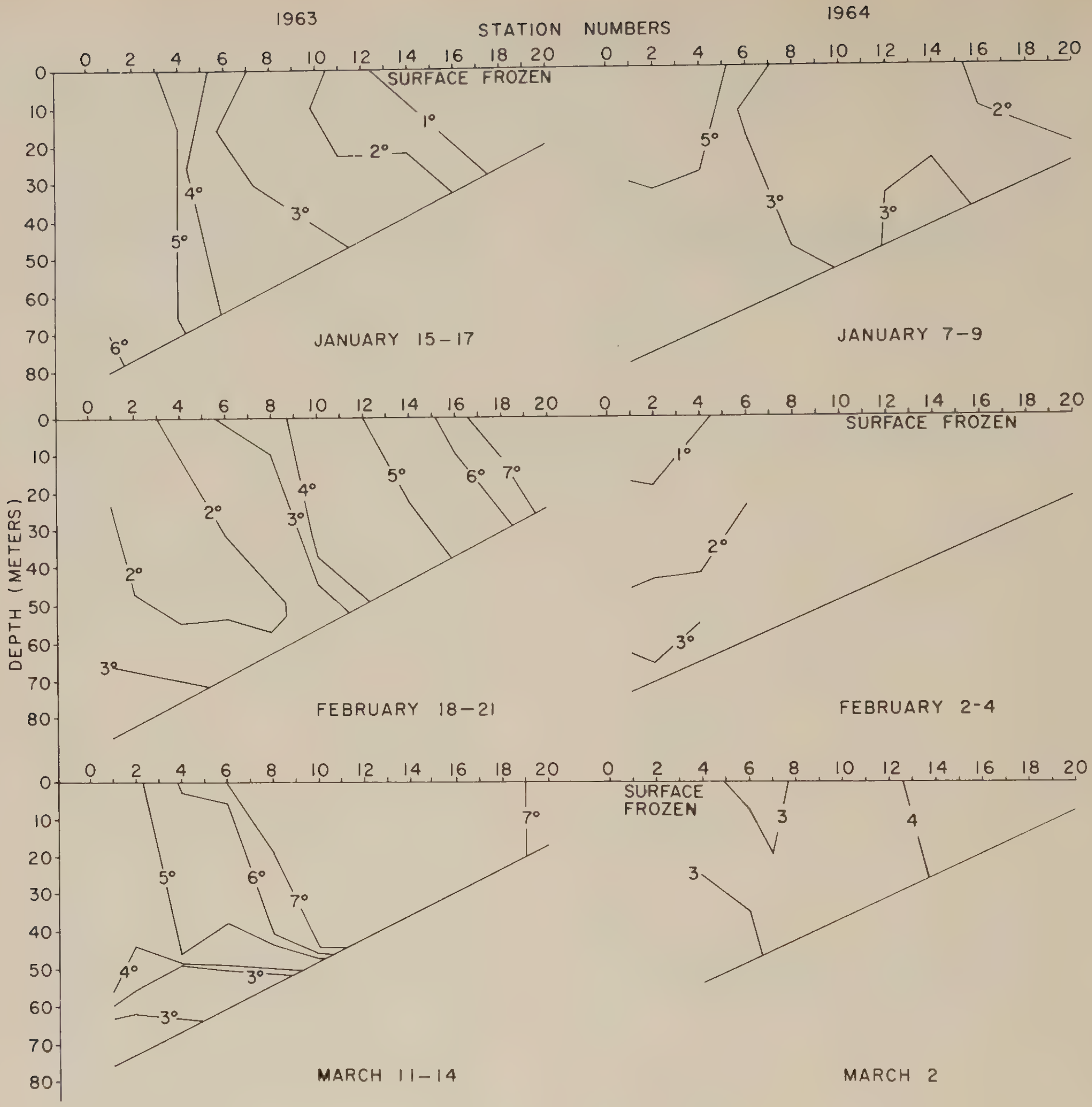


FIGURE 2.—Continued

tion and as mobile instruments to determine current patterns at any given time under any condition. Data were recorded under the following conditions: (1) during maximum reservoir drawdown; (2) at sustained minus 13-m. level with spill; (3) during fill-up without spill; (4) at full pool with high spill; and (5) at full pool without spill. The current meters, when used as continuous current recorders, were placed at midchannel stations in the lower, middle, and upper reservoir (I, II, and III, respectively, fig. 1) at a depth of 3 m. When the current meters were used as mobile instruments, measurements were made at the established limnological stations.

LABORATORY ANALYSES

Laboratory methods for analysis of samples followed standard methods (American Public Health Association, 1960). Quality control measures described for maintaining reagent normalities of sodium thiosulfate were also instituted and performed before each period. Sodium hydroxide, sulfuric acid, and reagents used in the field were checked immediately before each sampling period and renewed when necessary.

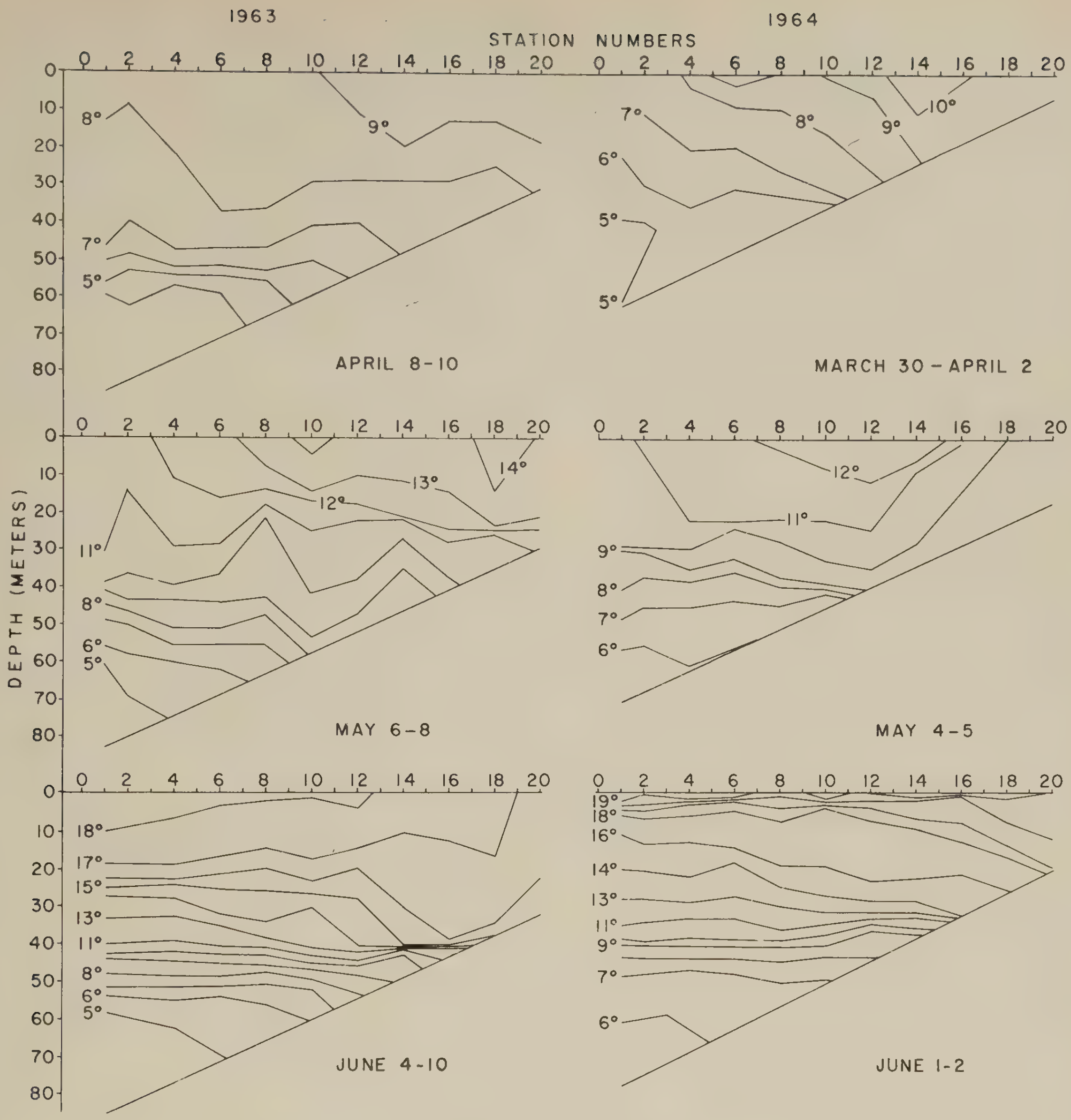


FIGURE 2.—Continued

PHYSICAL AND CHEMICAL PROPERTIES

Temperature, oxygen concentration, current, and other physical and chemical data are presented. Changes in these properties are described, and comparisons are made between years. Diurnal fluctuations of special interest are also described.

TEMPERATURES

The temperature regime of Brownlee Reservoir differs somewhat from that in large, deep lakes, but nevertheless shows the seasonal thermal changes of deeper lakes in the temperate zone: spring turnover, formation of thermocline, and fall turnover. In January 1963, the isotherms were vertical from upper reservoir to the dam (fig. 2). Temperatures in the upper portion ranged from 0.5° to 1.6° C.; those at the lower end ranged between 3.3° and 5.5° C. The isotherms remained vertical until mid-March; then the isotherms began to align horizontally at depths below 49 m. The January–March period is analogous in a

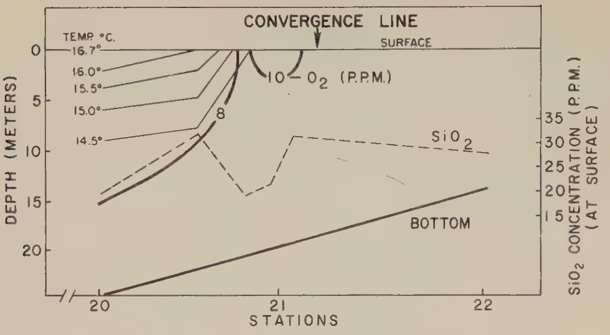


FIGURE 3.—Water temperature, oxygen concentrations, and silicon dioxide concentrations of Brownlee Reservoir from stations 20 to 22 at the time of formation of a visible convergence line, October 23, 1963.

sense to the "spring turnover" in lakes. Temperatures at this time ranged from 0.5° to 7.2° C.

Vertical stratification continued to strengthen after mid-March, and by early June a thermocline began to develop in the upper reservoir. Also in June, a visible convergence line (Frey, 1963) was observed in the upper reservoir near station 20. The cooler, heavier water from the Snake River dipped at this point and flowed under the warmer, lighter water of the reservoir. This condition was repeated in the fall (fig. 3). A sharp increase in temperature, higher concentration of oxygen (10 p.p.m.), and a dip in concentration of silicon dioxide were characteristic chemical and physical features observed in the vicinity of the convergence line in October 1963.

The temperature difference was 2.2° to 2.7° C. from one side of the convergence line to the other most of the time that the line could be identified. The temperature gradient near the visible line usually was extended over 0.8 km. The extreme difference of 2.7° C. during one sampling period, however, was from one side of the boat and the other. Turbidity readings and oxygen concentrations were higher upstream from the line, whereas conductivities were lower downstream. Wind action and the extent of discharge at the dam seemed to control the movement of the line upstream or downstream in the reservoir, as well as the sharpness of the temperature gradient.

The thermocline continued to develop during late spring and early summer of 1963; it was well defined from the upper reservoir to the dam by July 8. The stratification was then complete with a well-defined epilimnion, thermocline, and hypolimnion. Temperatures ranged from 15° to 25.5° C. in the epilimnion, 10° to 15.5° C. in the thermocline, and 3.9° to 9.5° C. in the hypolimnion.

Stratification continued until mid-October 1963, when the convergence or shear line was again formed. The heavier, cooler water from the river flowed under the warm epilimnion and evidently eroded the thermocline; distinct separation of isotherms was gradually eliminated until only a remnant of the thermocline remained in November. The reservoir was again in a state of turnover by December 9 when isotherms aligned vertically (fig. 2). Temperatures in the Powder River arm were nearly identical to those in the main reservoir.

The general patterns of the isotherms in 1962 and 1963 were similar except for time of formation of the thermocline. During the summer of 1962 a well-defined thermocline was not formed until early September, whereas in 1963 it was established by late June. Temperature ranges for the various months also differed; the greatest difference was in August. In 1962 the maximum was 27.2° C. whereas in 1963 it was 25.5° C. The temperature range for the epilimnion in August 1962 was 20.5° to 27.2° C.; in 1963 it was between 16.6° and 25.5° C. The reservoir temperatures gradually and consistently increased in 1962 without abrupt changes until September. In 1963 the trend was the same until the last of May, when a brief reversal occurred. The combination of heavy rain and melting snow in the headwaters caused a large volume of cool water to enter the Snake River above the reservoir (table 1). This mass of water cooled the entire upper end of the reservoir about 3.3° C. (see fig. 4).

Although air temperatures in June, July, and August 1962 were warmer than for the same period in 1963 (table 2), the thermocline developed earlier in 1963 than in 1962. The later formation of the thermocline in 1962 was due to the extent of reservoir drawdown and the length of the subsequent filling period. The drawdown in the winter of 1961 and ensuing months prolonged fill-up in the spring and early summer of 1962; it took place over a significant depth of 13.7 m. and caused enough water circulation to delay formation of the thermocline, despite the warmer air temperatures that year. By contrast, drawdown in the winter

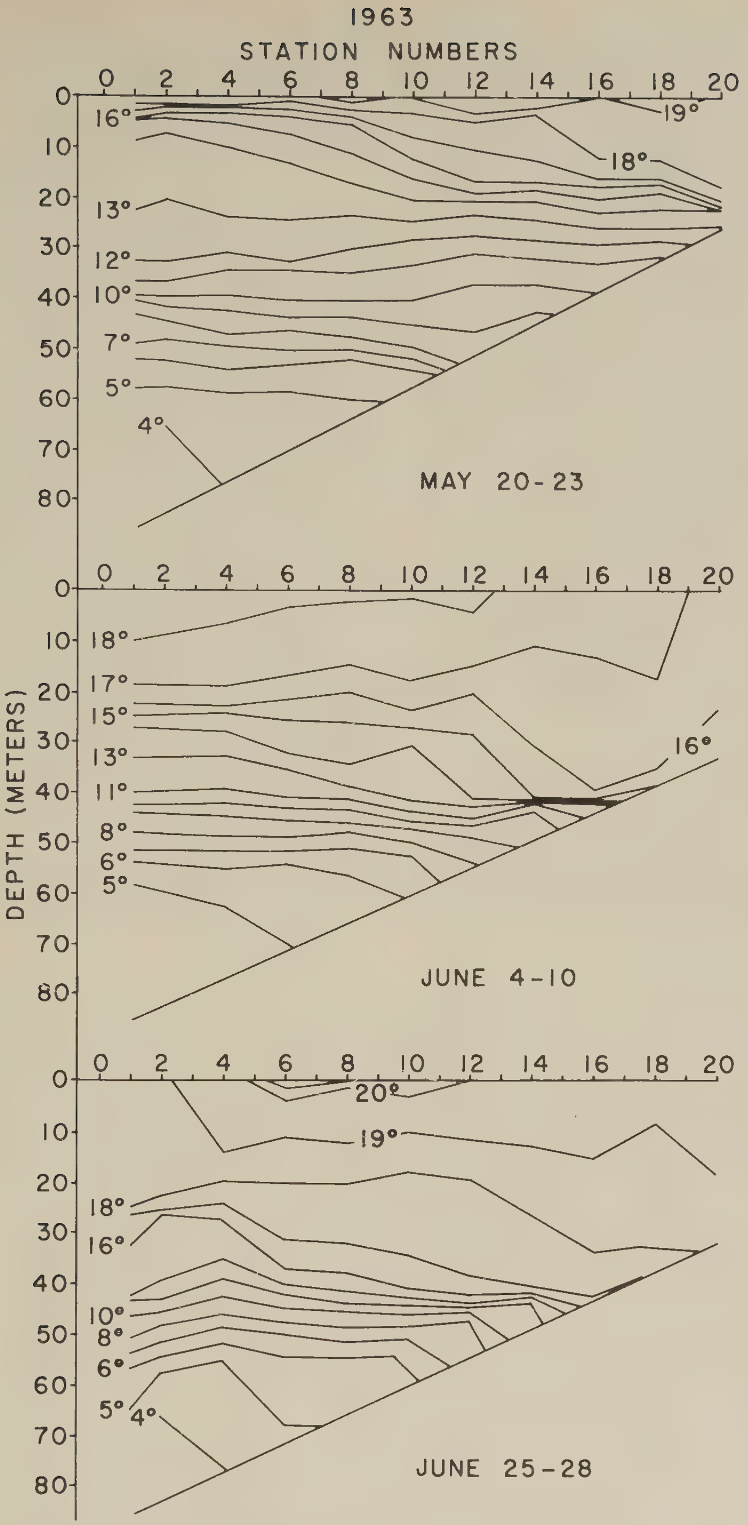


FIGURE 4.—Temperature isotherms (°C.), Brownlee Reservoir, May to June 1963. Cooling effect of cold river inflow is shown for June 4 to 10.

Table 1.—*Mean water temperature and mean volume of flow from the Snake River into Brownlee Reservoir and discharge at Brownlee Dam, May 1962 to June 1964*

Sample period	Mean temperature, Snake River at Weiser	Mean inflow at Brownlee	Mean discharge at Brownlee	Mean temperature at Brownlee[1] turbine outlets
1962	° *C.*	*C.m.s.*	*C.m.s.*	° *C.*
May 1–5	14.6	589.0	492.2	12.5
June 1–15	18.4	485.5	452.7	16.0
June 19–29	20.9	405.9	316.9	18.1
July 3–11	21.2	262.7	215.8	17.8
July 16–23	21.9	257.1	271.8	18.9
July 24–31	25.1	266.2	265.1	18.9
Aug. 6–10	23.3	314.9	389.6	20.4
Aug. 14–21	22.2	293.5	288.8	20.8
Aug. 22–28	22.2	293.0	268.2	21.1
Sept. 10–14	20.0	345.5	330.2	20.7
Sept. 25–Oct. 8	18.9	401.7	438.5	18.9
Oct. 10–16	13.9	510.5	453.1	16.9
Oct. 22–26	13.9	448.0	465.5	14.7
Nov. 26–30	7.5	442.9	418.5	10.3
Dec. 10–13	5.6	398.3	435.4	8.3
1963				
Jan. 15–17	5.6	341.9	542.1	6.1
Feb. 18–21	6.7	397.1	485.9	1.7
Mar. 11–14	8.9	371.7	379.3	4.7
Apr. 8–10	9.0	574.8	278.3	7.8
May 6–8	13.6	482.3	692.3	10.0
May 20–23	19.2	603.2	497.8	12.8
June 4–10	15.9	1,061.1	972.7	15.1
June 25–28	18.7	872.2	867.2	18.1
July 8–11	22.4	284.0	286.9	19.2
July 22–25	23.6	281.5	301.6	20.0
Aug. 6–9	23.1	296.6	288.7	20.0
Sept. 3–6	20.2	361.0	388.8	21.1
Oct. 1–3	16.7	366.2	401.6	20.0
Nov. 4–8	10.3	385.7	381.6	14.2
Dec. 9–12	4.4	387.2	444.6	7.7
1964				
Jan. 7–9	1.1	369.1	571.3	4.4
Feb. 2	3.3	371.0	401.8	3.3
Mar. 2	3.9	396.4	431.0	6.1
Mar. 30–Apr. 2	8.9	703.7	418.8	----------
May 4–5	11.7	773.1	835.7	----------
June 1–2	16.0	675.4	183.5	----------

[1] Courtesy of Bureau of Commercial Fisheries, River Basins Studies, Boise, Idaho.

of 1962 was relatively minor—only 6.4 m.; fill-up was short in 1963 and was completed by early May. As a result, the thermocline was formed fully 2 months earlier than in 1962.

OXYGEN CONCENTRATIONS

The chronological changes in oxygen concentrations permit description of seasonal changes and estimates at particular times (fig. 5).

Seasonal changes are described best by starting with January 1963, when dissolved oxygen concentrations approached saturation throughout the reservoir at all depths; conditions changed little until March when some decrease was evident below 49 m. Concentrations by May dropped to 1 p.p.m. on the bottom at stations 14 and 15, where the reservoir first receives a deposit of silt from the Snake River. Oxygen content of the entire reservoir ranged between 1 and 7 p.p.m.

Oxygen depletion continued at the lower depths from May until November when turnover began. The oxygen content near the surface (0–15 m.) increased in some areas, however, and generally ranged from 4 to 13 p.p.m. Increase of oxygen at the surface was presumably due to algae, which were readily visible throughout the reservoir. Lowest concentrations of oxygen came in August, when all water below 25 m. had a concentration of 3

Table 2.—*Air temperature at Weiser, Idaho,*[1] *and on west bank at station 14, Brownlee Reservoir, June 1962 to June 1964*

Locality and month	1962			1963			1964		
	Average maximum	Average minimum	Average median	Average maximum	Average minimum	Average median	Average maximum	Average minimum	Average median
	°*C.*	°*C.*	°*C.*	°*C.*	°*C.*	°*C.*	°*C.*	°*C.*	°*C.*
Weiser, Idaho:									
January				1.3	−8.5	−3.3	0.9	−9.8	−4.5
February				10.4	−.8	4.8	1.8	−12.5	−5.4
March				13.6	−.7	6.4	9.6	−3.2	3.2
April				15.4	1.8	8.6	12.3	1.4	6.8
May				23.9	6.6	15.2	22.4	4.6	13.6
June	29.2	9.4	19.3	25.5	9.6	17.6	25.6	9.2	17.4
July	32.2	13.3	22.7	31.6	9.5	20.6			
August	30.2	11.4	22.7	32.8	11.2	21.9			
September	26.5	6.8	16.7	28.7	9.2	19.0			
October	17.8	2.9	10.3	20.6	3.7	12.1			
November	10.1	−.6	4.8	9.9	−.8	4.5			
December	4.6	−2.2	1.2	.6	−7.5	−3.6			
Station 14, Brownlee Reservoir:									
January							2.9	−4.2	−.7
February				12.4	1.9	7.2	4.4	−4.3	.1
March				13.9	2.1	8.0	10.8	−.2	5.3
April				16.7	3.6	10.1	16.6	3.4	10.1
May				25.1	10.5	17.8	22.6	7.8	15.2
June				27.3	12.9	20.1	25.9	12.3	19.1
July				34.2	16.2	25.2			
August				34.5	18.4	26.4			
September				28.8	15.2	22.0			
October				22.2	17.9	20.1			
November				11.3	3.1	7.2			
December				3.0	−2.8	.1			

[1] Courtesy of radio station KWEI.

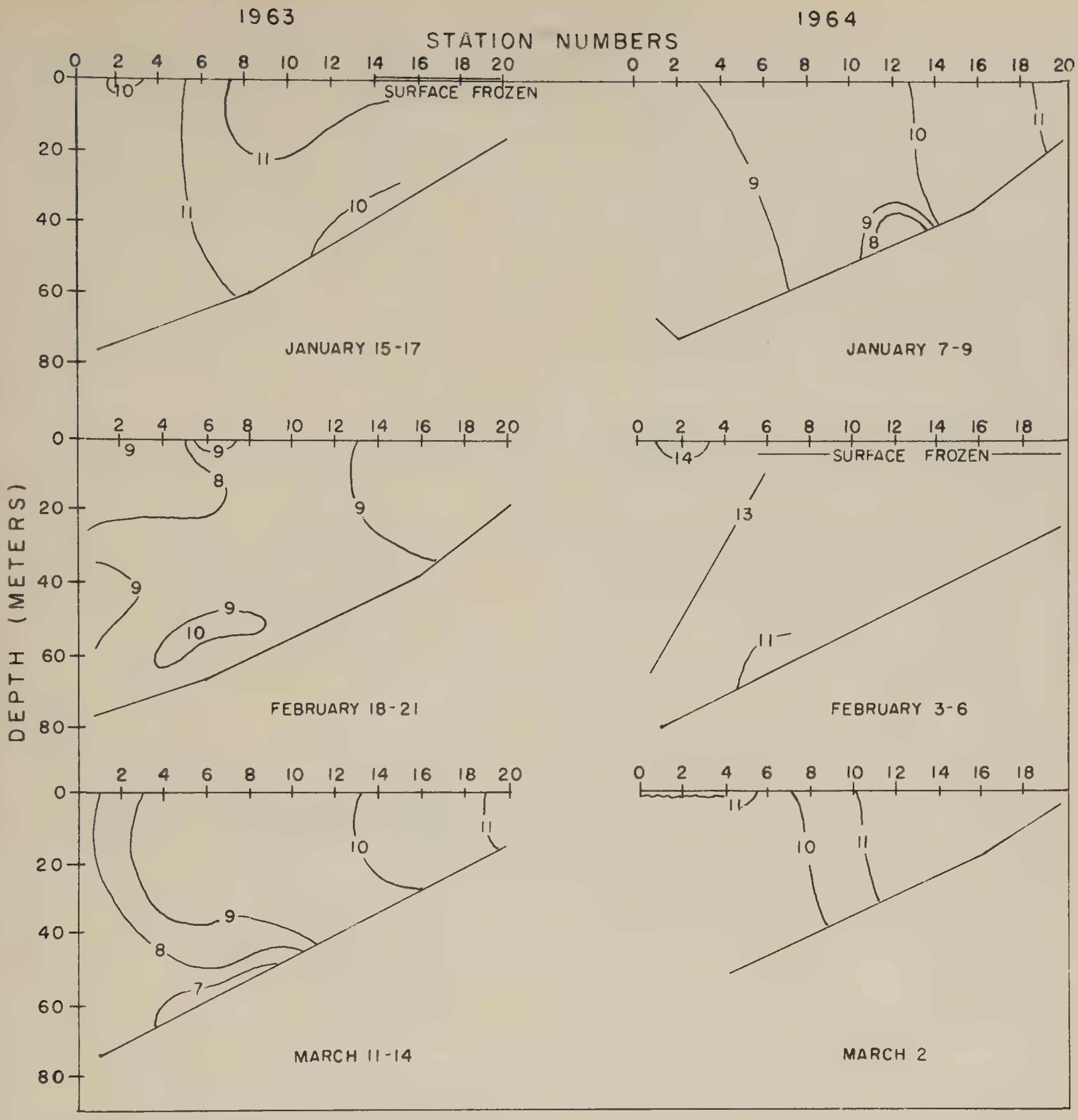


FIGURE 5.—Dissolved oxygen (p.p.m.) profiles, Brownlee Reservoir. Comparison of months for July 1962 to June 1964.

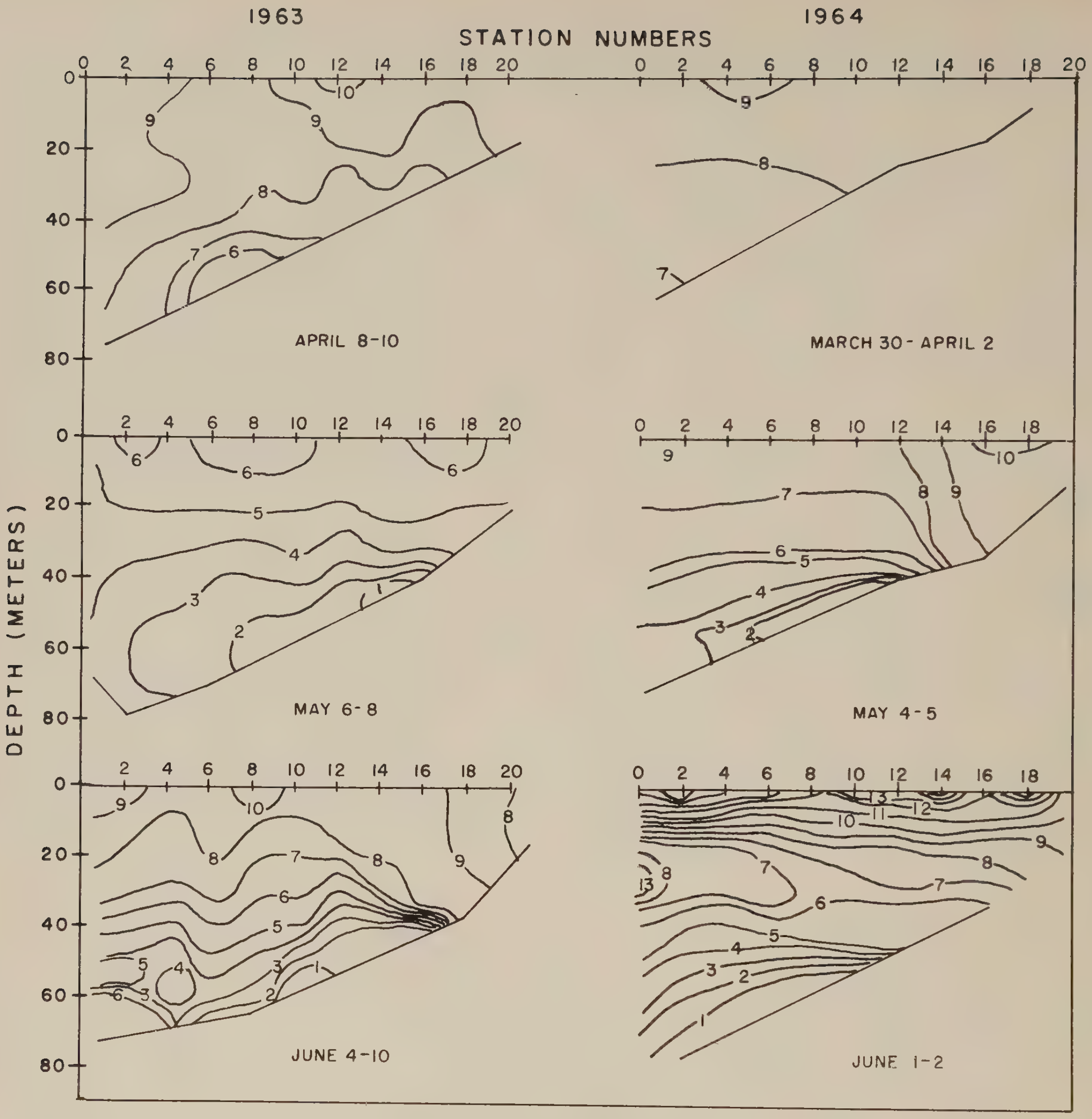


FIGURE 5.—Continued

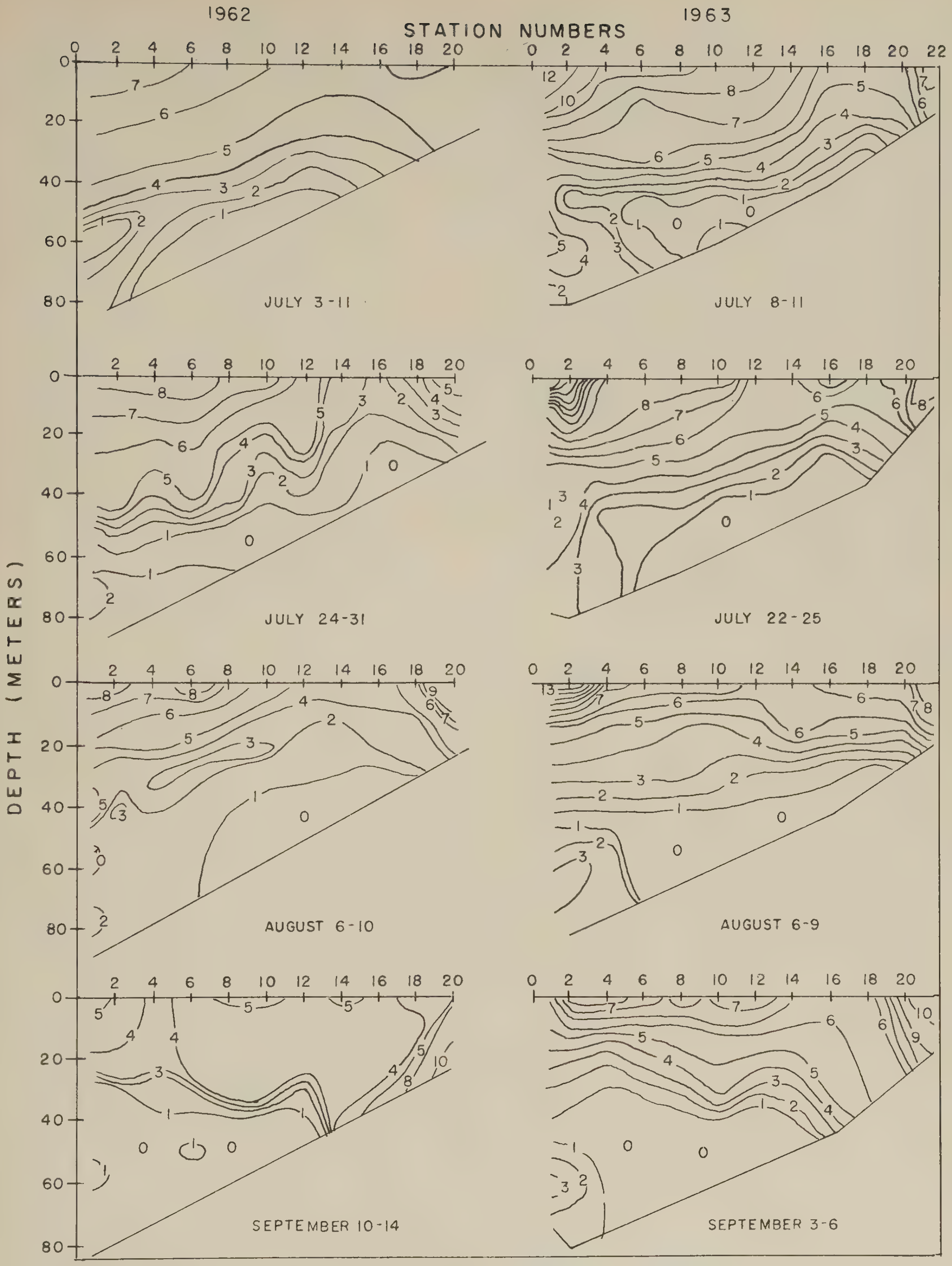
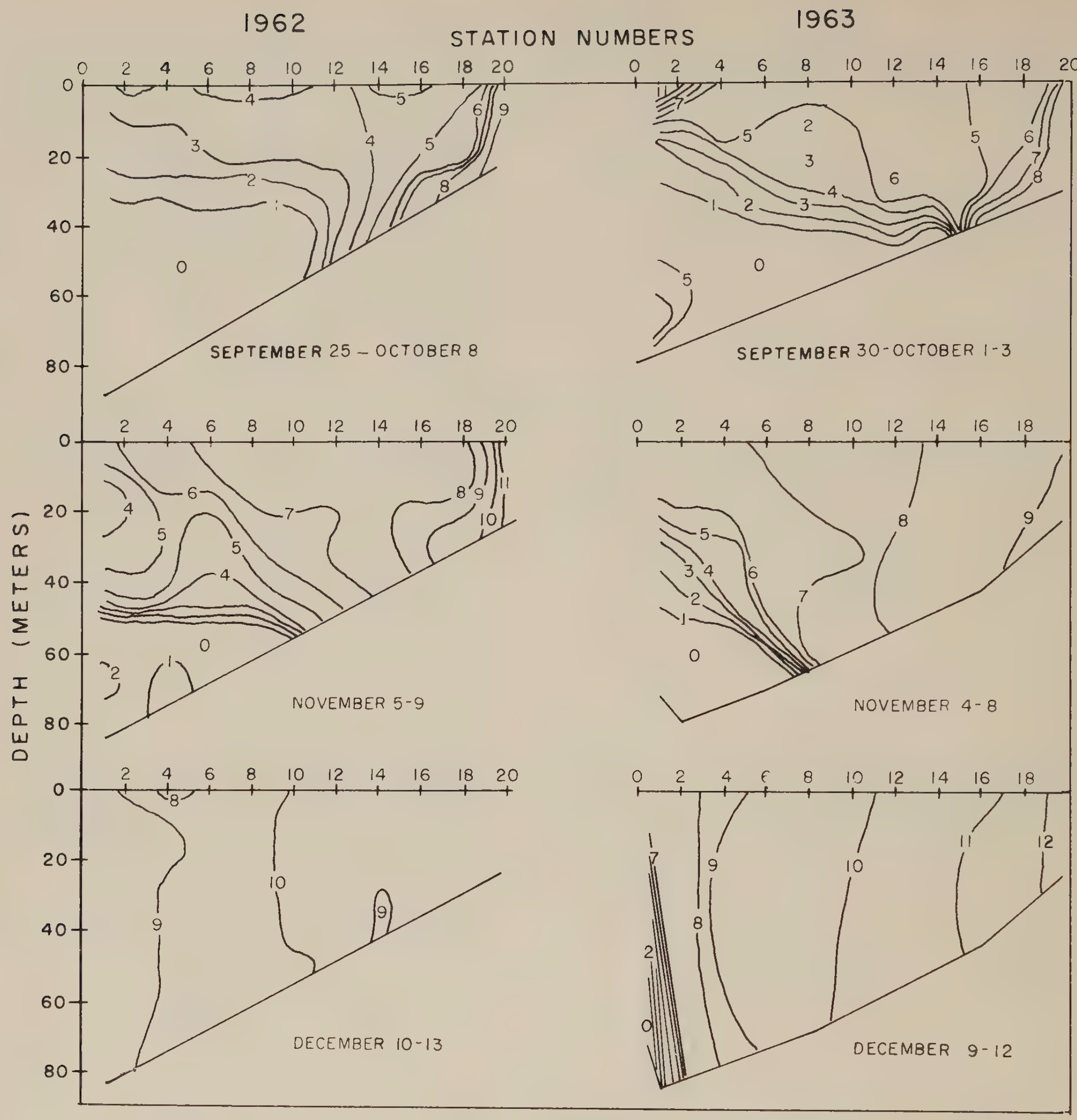


FIGURE 5.—Continued



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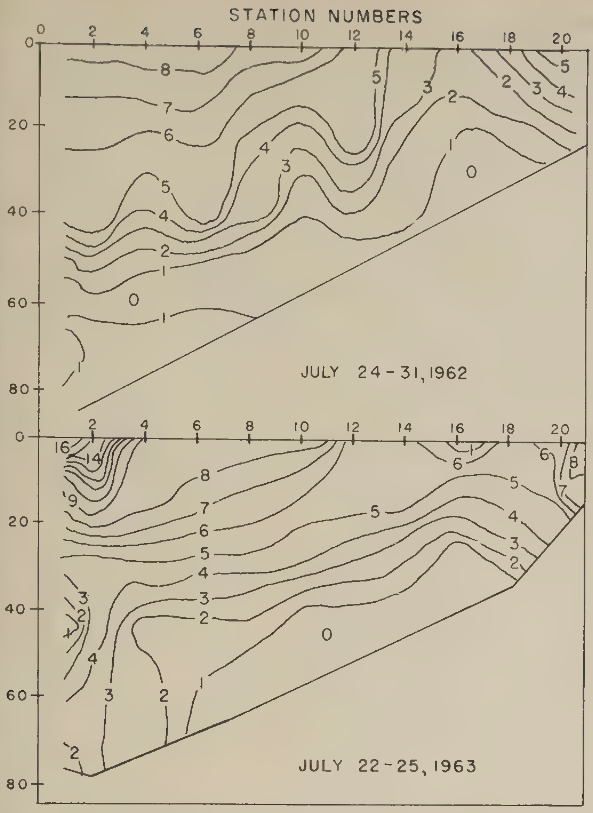


FIGURE 6.—Comparison of oxygen concentrations in Brownlee Reservoir July 1962 and July 1963. Note pronounced oxygen block at upper end of reservoir (stations 14 to 18) in 1962.

p.p.m., or less, and most of the water below 15 m. had 4 p.p.m. or less. This condition persisted through September but was alleviated somewhat in the upper end of the reservoir by October because of cooler inflow from the Snake and Burnt Rivers. By November, nearly two-thirds of the reservoir water contained 7 to 9 p.p.m. dissolved oxygen.

A small remnant of the hypolimnion remained at the dam in December, but more than nine-tenths of the reservoir had completely overturned; oxygen concentrations ranged from 7 to 12 p.p.m. Concentration changes were similar in the Powder River arm.

Oxygen records indicated that location of the turbine intake at 37 m. below normal pool level created sufficient circulation adjacent to the dam to bring some of the oxygenated water from the epilimnion down to the hypolimnion from July through October. Oxygen concentrations in this area for the same months in 1962 were almost identical.

An oxygen block or area of oxygen depletion (fig. 6) similar to that described by Fish and Wagner (1950) and Ellis (1942) was present in late July, 1962; it could be traced progressively through the reservoir in successive months (fig. 5). This block was not observed in 1963, although some evidence suggested that it was beginning to form. Shortly thereafter, the incipient block disintegrated.

Another major difference in the graphs of oxygen concentrations is that concentrations in September 1962 were considerably lower in the epilimnial waters than they were during the same month in 1963. Very possibly the oxygen block, higher air temperatures, and lower inflow from the Snake River all contributed to the lower epilimnial concentrations of oxygen in September 1962.

CONDUCTIVITY, pH, AND OTHER CHEMICAL PROPERTIES

Total alkalinity, phenolphthalein alkalinity, carbon dioxide, hydrogen-ion concentration, silicon dioxide, sulphates, turbidity, and conductivity were obtained for the surface, middepth, and bottom. Ranges for each year are presented; variation with depth, during the year and from one year to the other, is described.

Alkalinity was generally similar for comparable periods during the 27 months of study. Concentrations (fig. 7) ranged from 68 to 202 p.p.m. for 1962–63 and from 86 to 225 p.p.m. for 1963–64. Concentrations were highest in December, January, February, and March; they were lowest during May and June and increased through one summer. These concentrations were undoubtedly governed in part by the trend in alkalinity in the Snake River and in other tributaries (table 3). Alkalinity concentrations were fairly uniform during December and January when the reservoir was nearly homothermous and oxygen concentrations were nearly uniform. Range in concentrations was widest during the summer, when the reservoir was stratified.

The highest alkalinity occurred in the hypolimnion during June, July, and August. Precipitation of normal carbonates by aquatic organisms and

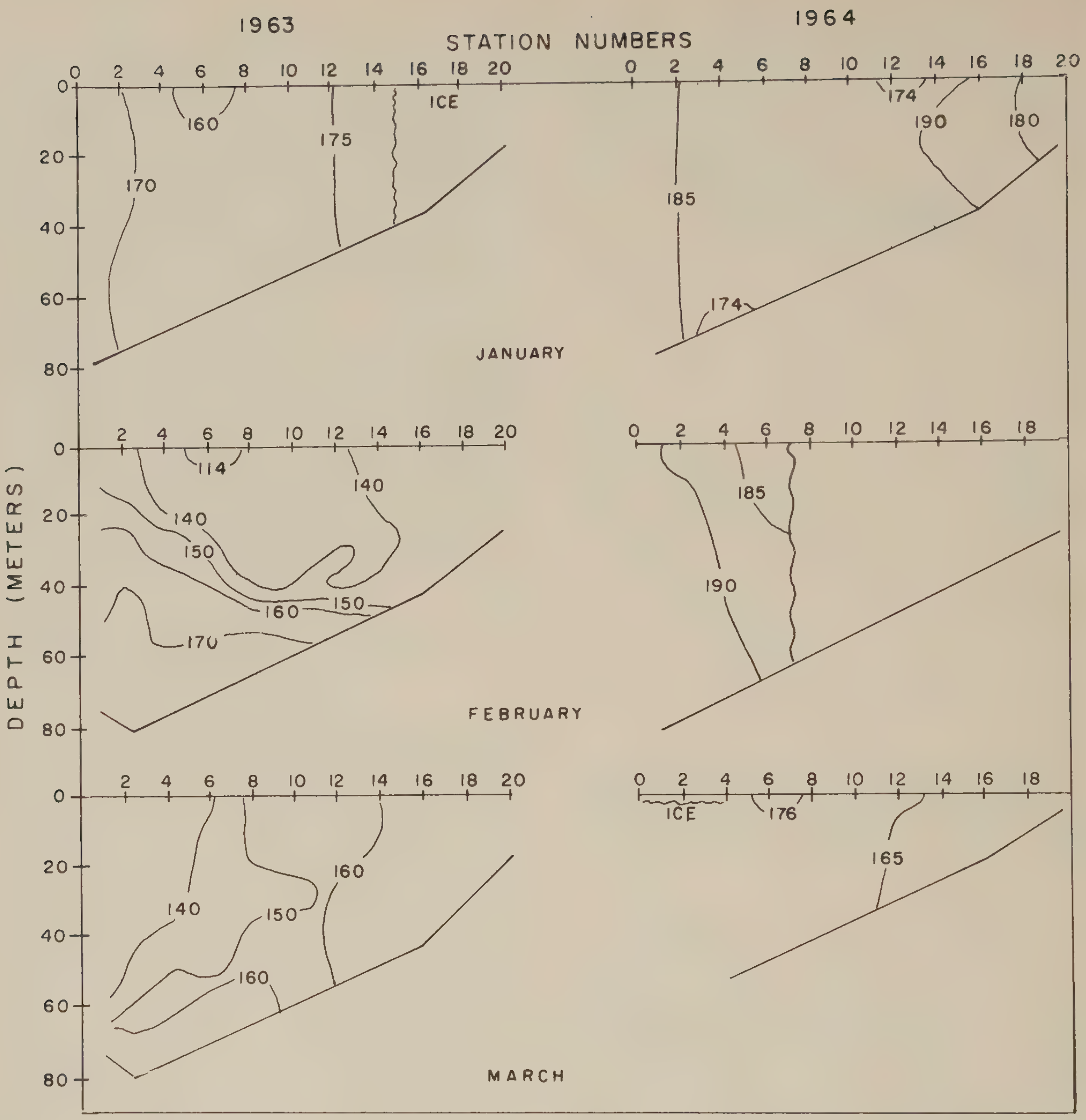


FIGURE 7.—Total alkalinity (p.p.m.), Brownlee Reservoir, July to December 1962 and 1963 and January to June 1963 and 1964.

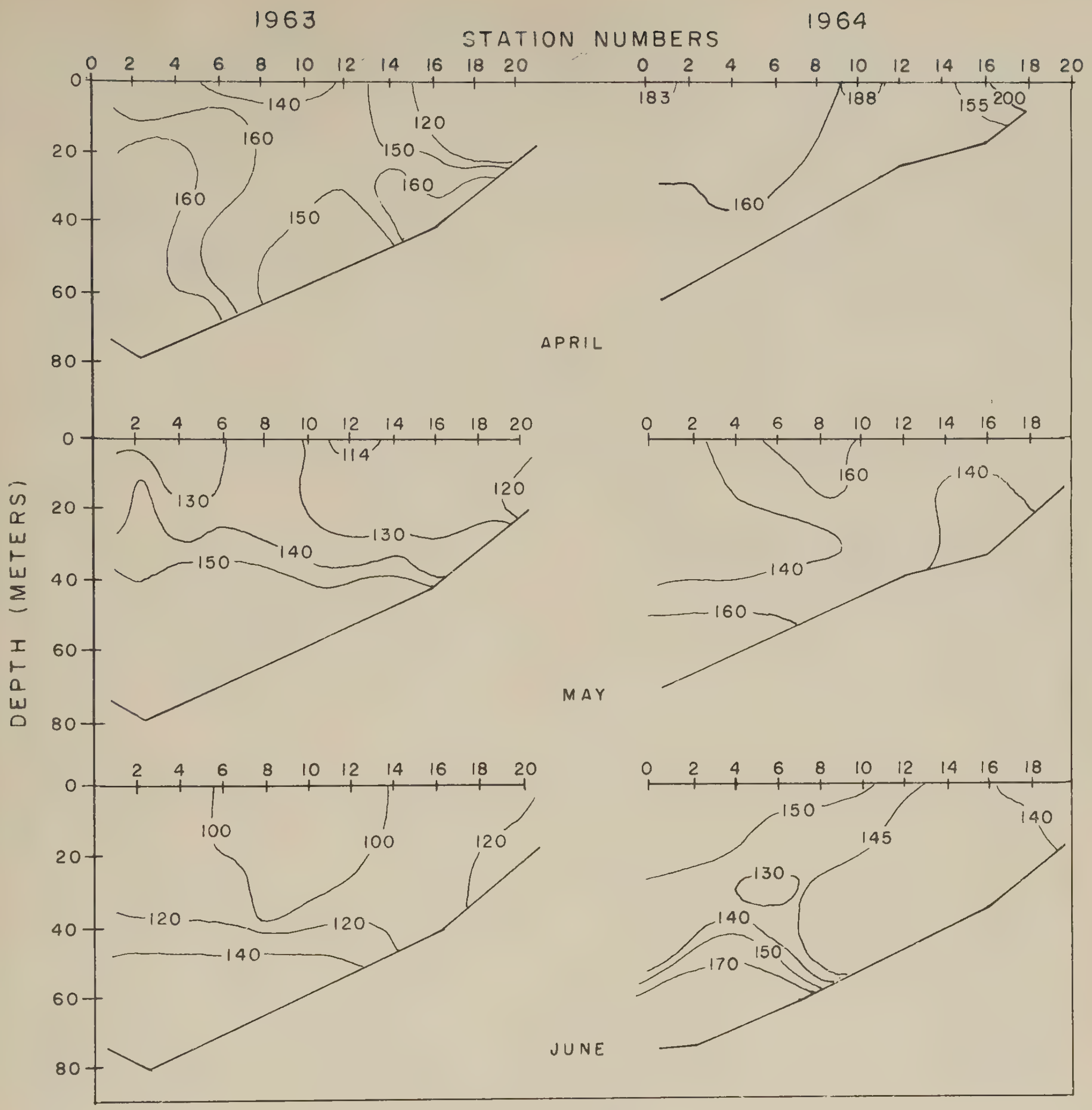


FIGURE 7.—Continued

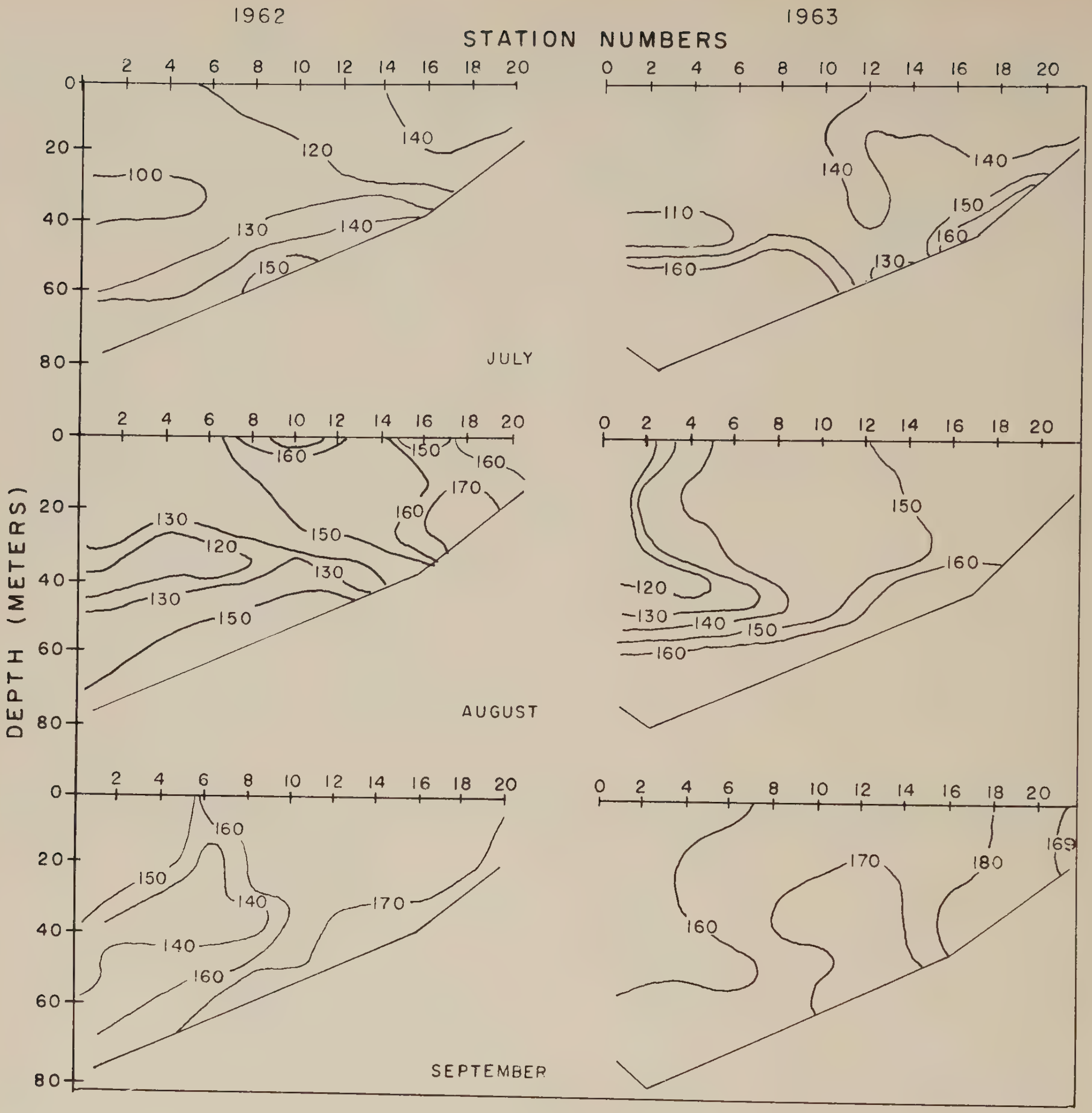


FIGURE 7.—Continued

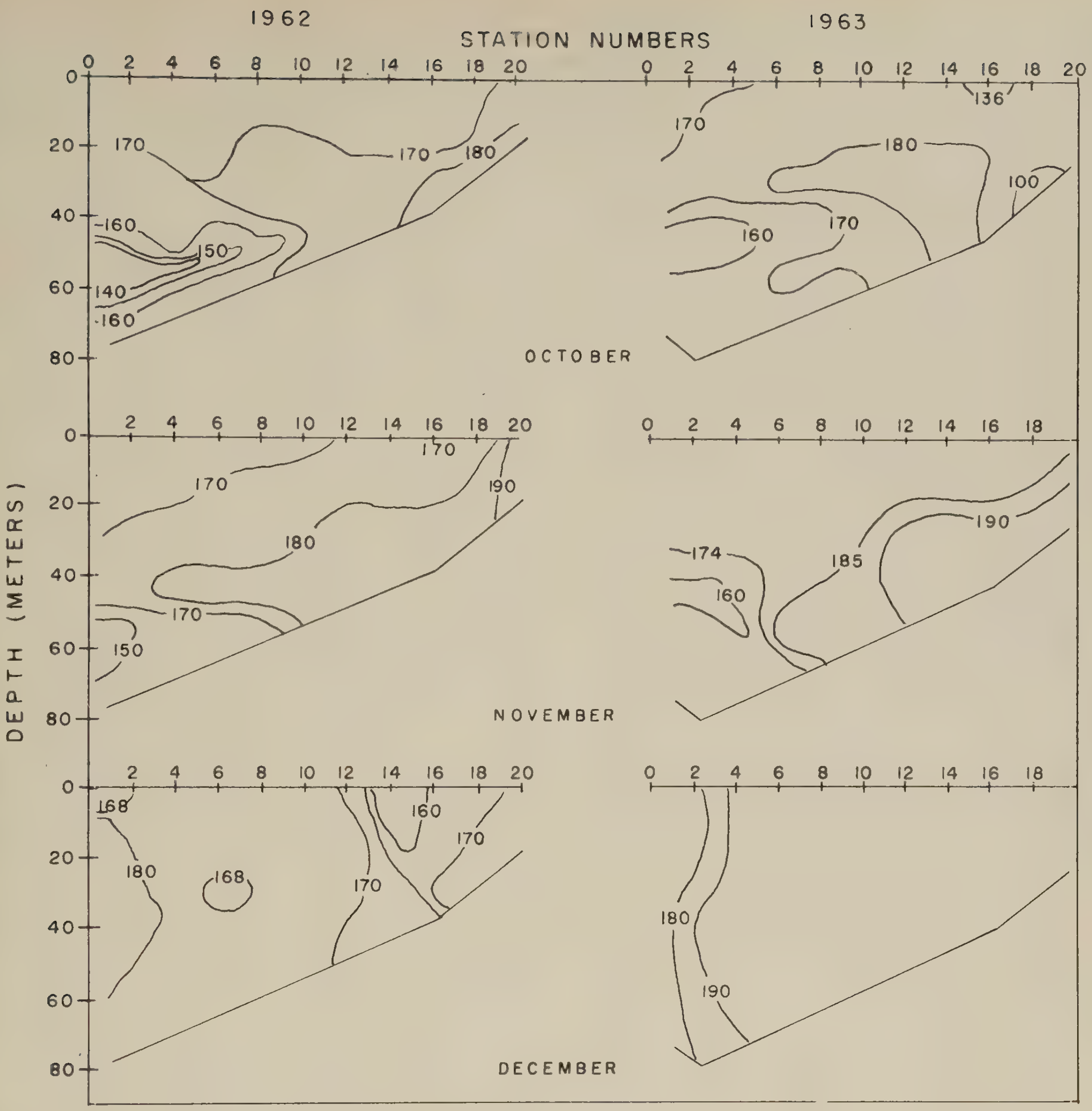


FIGURE 7.—Continued

Table 3.—*Surface temperature and chemical characteristics of water in Snake River (at Weiser, Idaho), Powder River, and Eagle Creek, January 1963 to June 1964*

Year and month	Total alkalinity	Phenolphthalein alkalinity	CO_2	pH	Temperature	O_2	SO_4	SiO_2
Snake River:								
1963:	*P.p.m.*	*P.p.m.*	*P.p.m.*		*°C.*	*P.p.m.*	*P.p.m.*	*P.p.m.*
January	175	5	0.0	8.6	5.6	11.6	35	6
February	147	2	.0	----------	6.7	10.0	46	61
March	168	12	.0	----------	8.3	11.4	43	47
April	141	9	.0	8.4	8.9	11.5	39	31
May	119	12	.0	----------	14.4	8.9	8	34
June	115	12	.0	----------	21.7	10.1	6	15
July	139	15	.0	----------	23.3	10.8	12	58
August	176	0	6.2	7.5	23.3	6.6	53	40
September	175	0	2.6	7.8	21.7	8.0	54	83
October	186	6	.0	7.6	16.7	9.0	43	34
November	190	13	.0	8.1	10.0	10.3	58	28
December	191	15	.0	8.2	4.4	12.2	46	50
1964:								
January	180	1	.0	8.6	.6	13.1	51	39
February	179	13	.0	8.2	3.3	15.4	50	47
March	169	4	.0	7.8	3.9	11.2	42	52
April	99	3	.0	7.7	7.8	9.7	29	7
May	171	6	.0	8.5	11.7	9.8	51	8
June	130	14	.0	----------	15.6	11.2	34	64
Powder River:								
1963:								
January	----------	----------	----------	----------	----------	----------	----------	----------
February	104	0	4.4	7.7	3.3	11.7	22.5	67
March	109	0	[1] 4.0	7.7	5.0	11.6	7.0	66
April	122	0	1.8	7.7	7.2	14.1	3.0	36
May	149	10	.0	8.1	16.1	8.7	1.5	54
June	185	11	.0	8.1	26.7	7.3	9.0	125
July	209	14	.0	[1] 8.8	24.4	8.7	1.5	15
August	265	12	.0	[1] 8.5	27.8	7.2	22.0	22
September	265	9	.0	8.0	25.6	8.2	13.0	25
October	239	14	.0	[1] 8.5	14.4	11.0	18.0	15
November	224	22	.0	[1] 8.9	9.4	12.0	19.0	31
December	181	0	4.4	8.0	2.2	12.6	36.0	58
1964:								
January	Frozen	----------	----------	----------	----------	----------	----------	----------
February	150	6	.0	8.0	2.2	16.7	20.0	25
March	136	[1] 5	.0	8.4	5.6	13.9	5.5	36
April	82	0	2.0	7.6	----------	10.2	125.0	60
May	136	1	.0	8.2	15.6	10.6	42.0	11
June	150	0	7.0	----------	14.4	8.6	11.0	74
Eagle Creek:								
1963:								
January	64	0	[1] 7.0	7.4	4.4	12.1	6.0	3
February	66	0	3.5	7.8	3.3	12.4	5.0	16
March	69	0	[1] 6.0	7.3	5.0	12.2	3.5	25
April	68	0	1.8	7.4	6.1	9.9	3.5	10
May	56	0	1.8	7.0	11.7	10.2	1.0	19
June	29	0	3.5	7.2	15.0	9.8	1.0	45
July	58	[1] 0	.0	7.1	21.1	8.4	1.0	6
August	151	0	2.6	7.6	27.8	6.7	3.0	19
September	149	9	.0	8.2	27.8	9.7	3.0	42
October	146	0	15.0	7.2	18.3	8.8	3.5	19
November	85	[1] 0	.0	7.8	10.0	10.7	4.0	36
December	87	0	3.5	7.5	3.3	12.2	2.0	42
1964:								
January	100	0	7.9	7.9	1.1	13.0	4.5	39
February	86	[1] 6	.0	7.6	2.2	15.5	8.0	22
March	78	6	.0	8.0	6.7	12.6	1.5	26
April	62	[1] 0	.0	7.6	8.9	10.8	8.0	35
May	75	1	.0	8.1	14.4	10.6	25.0	11
June	36	0	4.0	----------	8.3	10.6	4.5	34

[1] Computed from Moore (1938).

their subsequent conversion to bicarbonate by carbonic acid probably accounted for the higher readings. The large local variation in the concentration was probably caused by currents, algae, and changes in alkalinity of the inflowing river.

The samples were also analyzed for normal carbonate. Concentrations for July 1962 through June 1963 ranged from 0 to 30 p.p.m.; for 1963–64, the range was 0 to 21 p.p.m. Maximum concentrations were in the surface layer (0–15.2 m.). The lower depths contained no normal carbonate during July and August, when production of algae was high and stratification complete. This condition was similar to that in lakes described by Welch (1952). Decomposition of algae and other organic material at the lower depths apparently liberated enough carbon dioxide to convert all carbonate to bicarbonate. This assumption is supported by the fact that concentrations of high carbon dioxide were at the lower depths.

Concentrations of carbon dioxide were low in the spring and early summer, but high in the fall. Free carbon dioxide was lacking in January of both years. The range in concentration (p.p.m.) for 1962–63 (July–June) was 0 to 12 for the surface, 0 to 11 for the 30.5- to 45.7-m. layer, and 0 to 19 for the 45.7-m. layer to the bottom. The ranges for 1963–64 were 0 to 19, 0 to 23, and 0 to 43 for the surface, middepth, and bottom. Highest values were at the lower depths. Concentrations were not only far below the lethal levels indicated by Ellis (1937) but usually below the harmful level (39.2 p.p.m.) indicated by McKee and Wolf (1963).

Hydrogen-ion concentration (pH) in the reservoir ranged from 7 to 8.9. The high pH of the Snake River (table 3) throughout the year accounted for the high readings in the reservoir. The readings were highest in surface water where concentrations of normal carbonate were highest. The range in pH of the surface water in 1963, for example, was 7.7 to 8.9, but the range at lower depths, 46 m. to bottom, was 7 to 8.3. Neutral values of 7 were typical near the bottom during August and September, when the reservoir was well stratified. Decomposition of organic material apparently liberated enough carbon dioxide into the hypolimnion to lower the pH to this level. Concentrations were slightly higher on the bottom during these same 2 months in 1962. The pH ranged from 7.5 to 8.5 throughout the year in most of the water mass, indicating that Brownlee Reservoir is relatively alkaline in comparison with other lakes and reservoirs in the United States.

Conductivity readings, which were adjusted to 20° C., ranged from 253 to 867 micromhos. Values were low in the spring, progressively higher during the summer, and low again in the late fall after the turnover. During stratification, the highest readings were usually in the surface layer and the lowest readings in the hypolimnion. This phenomenon is the reverse of what would be expected if conductivity fluctuated with total alkalinity. Conformity with the expected relation (when the highest conductivity readings were in the hypolimnion) existed only in July and August of 1962 and 1963 and only in the lower part of the reservoir. Apparently some electrolytic substance, other than those sampled, was reduced at the lower depths. Ellis (1940) found that conductivities paralleled alkalinities and sulfates and that all three were higher at the lower depths. Although conductivity reached 867 micromhos, this figure was still below the level

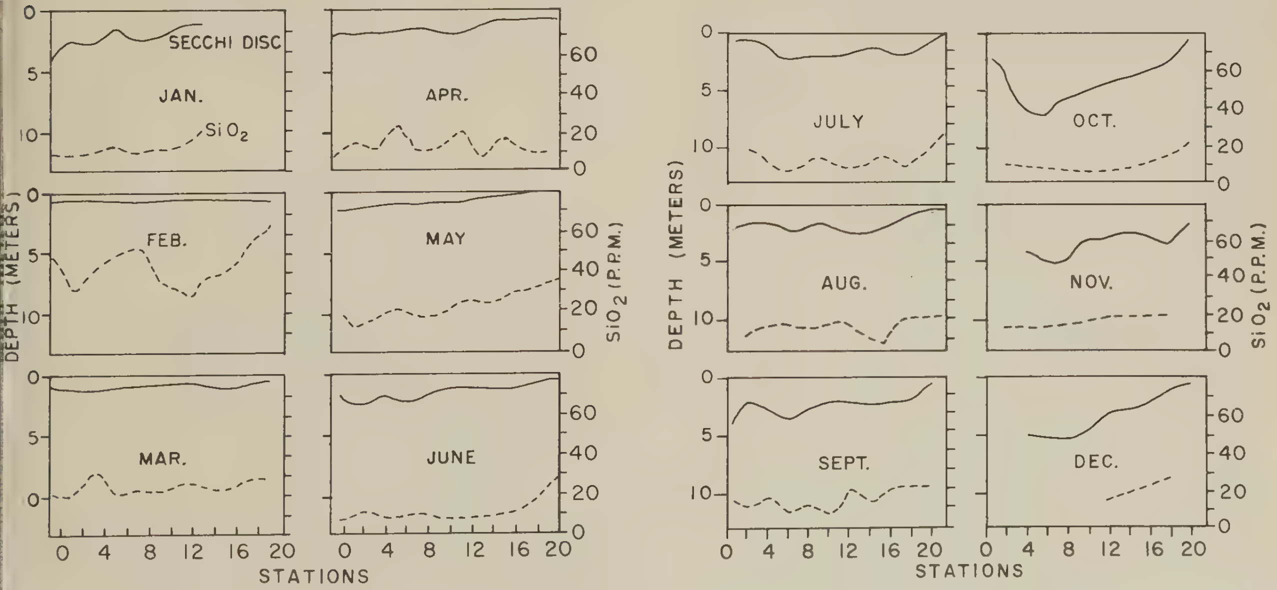


FIGURE 8.—Comparison of Secchi disc readings (solid lines) and surface silicon dioxide concentrations (broken lines) in Brownlee Reservoir, January to December 1963.

(1,000) set by Ellis (1944) as the upper limit of conditions favorable to fish life.

The range in sulfate concentrations for July 1962 to June 1964 was 2 to 69 p.p.m. The value throughout the reservoir was 15 to 50 p.p.m. during most of the year, which is considered the optimum range for aquatic life (McKee and Wolf, 1963). Sulfate concentrations were highest in the surface waters and lowest in the deeper waters during most of the year. This distribution may account in part for the lower conductivities at the lower depths mentioned earlier.

Secchi disc readings and silicon dioxide concentrations for 1963 are shown in figure 8; the readings were typically low when silicon dioxide concentrations were high. Turbidity showed an annual cycle comparable to that of total alkalinity and was greatest in February (Secchi disc 0.3–0.6 m.) during drawdown, when silt deposited in the upper reservoir was recirculated by the turbulent river inflow. Turbidity continued high throughout the spring and early summer and then gradually decreased through the fall. The highest Secchi disc readings (lowest turbidity) were in October at stations 4 and 6 (7.1 and 7.6 m.). The Snake River above Brownlee Reservoir remained turbid throughout the year; the maximum reading in the river was 0.6 m. Hence, the uppermost portion of the reservoir was always rather turbid.

Several authors have analyzed the relation between turbidity and plankton production and, hence, with fish production. Their conclusions vary depending on the characteristics of the water mass studied and on their interpretation of available data. For example, Van Oosten (1948) found no correlation, whereas Langlois (1941) indicated a high correlation. The large phytoplankton blooms on the surface of Brownlee Reservoir throughout the summer indicated that high turbidity did not seriously hinder primary production near the surface.

DIURNAL OBSERVATIONS OF LIMNOLOGICAL CONDITIONS AND CONDITIONS AT TRAP SITES

Four diurnal studies were carried out from June 1962 to June 1964 to measure fluctuations under unusual conditions during mortalities at a fingerling trap site, or to determine diurnal fluctuations at the end of winter or in late summer. Studies were made September 5 and 6, 1962, July 17 and 18, August 19 and 20, 1963, and May 12 and 13, 1964. The studies in the early spring (May 1964) and late summer (September 1962) showed that diurnal variations in temperature and water chemistry were minor. Temperatures in the reservoir in September and May did not change more than 1.1° C. Maximum change in oxygen concentration was 1.3 p.p.m. in September and 3 p.p.m. in May. Changes in concentrations of other factors were similarly minor.

The diurnal observation at a floating fish trap at station 18 was done to determine if water temperature and chemistry contributed to the high mortality of young salmon captured on July 17, 1963. Samples were taken at 1500 hours on July 18 and every 3 hours over the ensuing 24-hour period at the trap and at a point 30 m. outward from it. The samples at the two sites did not differ significantly. Water temperatures ranged from 22.1° to 23° C. at the 6-m. level and from 22.3° to 23.3° C. at the surface. Diurnal variation was 1.1° to 1.65° C. at the surface; the temperature was highest in the early afternoon. Dissolved oxygen concentrations ranged from 3.2 p.p.m. to 2 p.p.m. on the surface and from 2.1 p.p.m. to 1.6 p.p.m. at the 6-m. level. No cyclic trend in oxygen concentrations appeared. The high temperatures and the low dissolved oxygen concentrations apparently were major factors in the high mortality of captured fish. Concentrations of pH, carbon dioxide, and sulfates were suitable for survival of fish (Ellis, 1937, 1944); diurnal fluctuations were lacking.

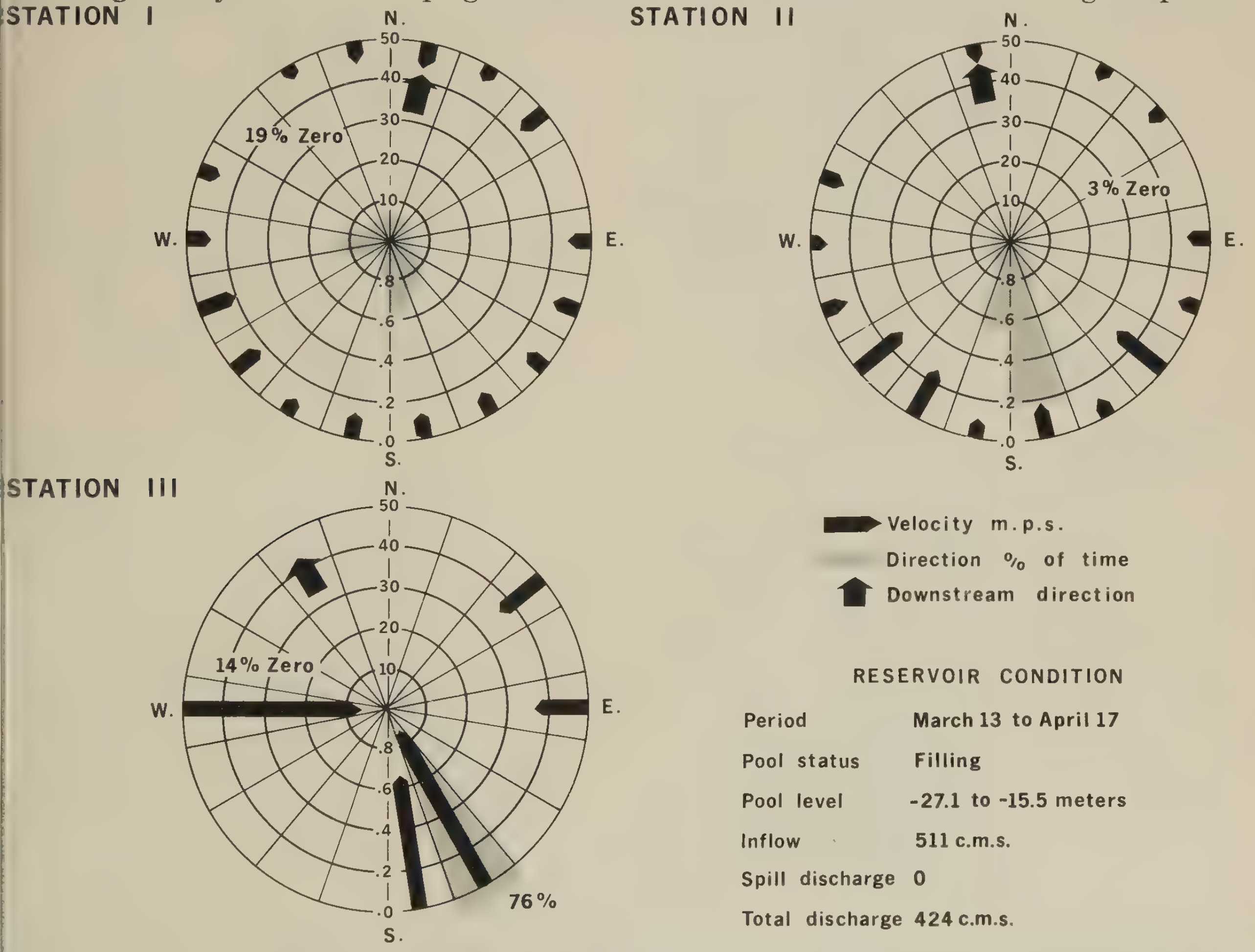
A day-night study also was done in the Powder River arm of Brownlee Reservoir on August 19 and 20, 1963. The purpose was to determine the extent of diurnal variation in water chemistry and temperature in an area of high concentrations of algae. A series of samples was taken from the surface to the bottom at stations PR4 (PR4 located midway between PR3 and PR5) and PR5, in a relatively shallow pond at the head of the arm, and at station PR3, at midarm. Surface water temperatures varied 2.3° C. through the day-night cycle, ranging from 20.5° to 22.8° C. Diurnal fluctuation in dissolved oxygen concentrations at the three stations was high; maximum variation at the surface was at PR4, where the range was 6.8 to 14 p.p.m. Concentrations were high in the late afternoon when algal activity was greatest. Concentration of dissolved oxygen at the surface dropped to 5.6 p.p.m. at station PR5 in the early morning hours.

Free carbon dioxide concentrations were 3.5 to 12.3 p.p.m. from 9 to 15 m. in all samples at station PR3, and no diurnal change was apparent. Hydrogen-ion concentrations ranged from 7.4 to 8.3 in the surface waters at all stations.

Additional limnological sampling was done throughout March, April, and May 1963 at sites of surface trap nets to measure limnological conditions at each trap during the peak migrations of salmon fingerlings. All sampling was during daylight, normally between 0800 and 1600 hours. Oxygen concentrations remained saturated or near saturation (8–15 p.p.m.). Water temperatures warmed gradually as the season progressed but remained favorable for fish until the end of May, when they rose to 23.9° C. All chemical determinations were within acceptable limits for fish. Samples taken at the trap sites did not differ appreciably from those taken at established stations in the same general areas of the reservoir.

CURRENTS

Continuous and instantaneous current measurements are discussed in this section as well as wind and other factors that affect surface currents. Surface currents were considered of primary importance because most of the fingerling migrants remained near the surface during the peak of the downstream migration. Surface currents were, therefore, recorded continuously to provide an accurate description during any period. Instantaneous measurements were made during five periods



RESERVOIR CONDITION

Period	March 13 to April 17
Pool status	Filling
Pool level	-27.1 to -15.5 meters
Inflow	511 c.m.s.
Spill discharge	0
Total discharge	424 c.m.s.

FIGURE 9.—Direction (percentage of time, indicated by scale between center and upper margin of each figure) and average velocity (m.p.s. scale between center and lower margin) of currents recorded at 3-m. depth in Brownlee Reservoir during maximum drawdown, March 13 to April 17, 1964. Direction of current reads toward point of wedge.

at times of major changes in reservoir conditions. These periods are the same as those described under continuous recording except for the period described as fill-up at minus 20.4 m. from full pool level. The instantaneous measurements provide information on subsurface currents.

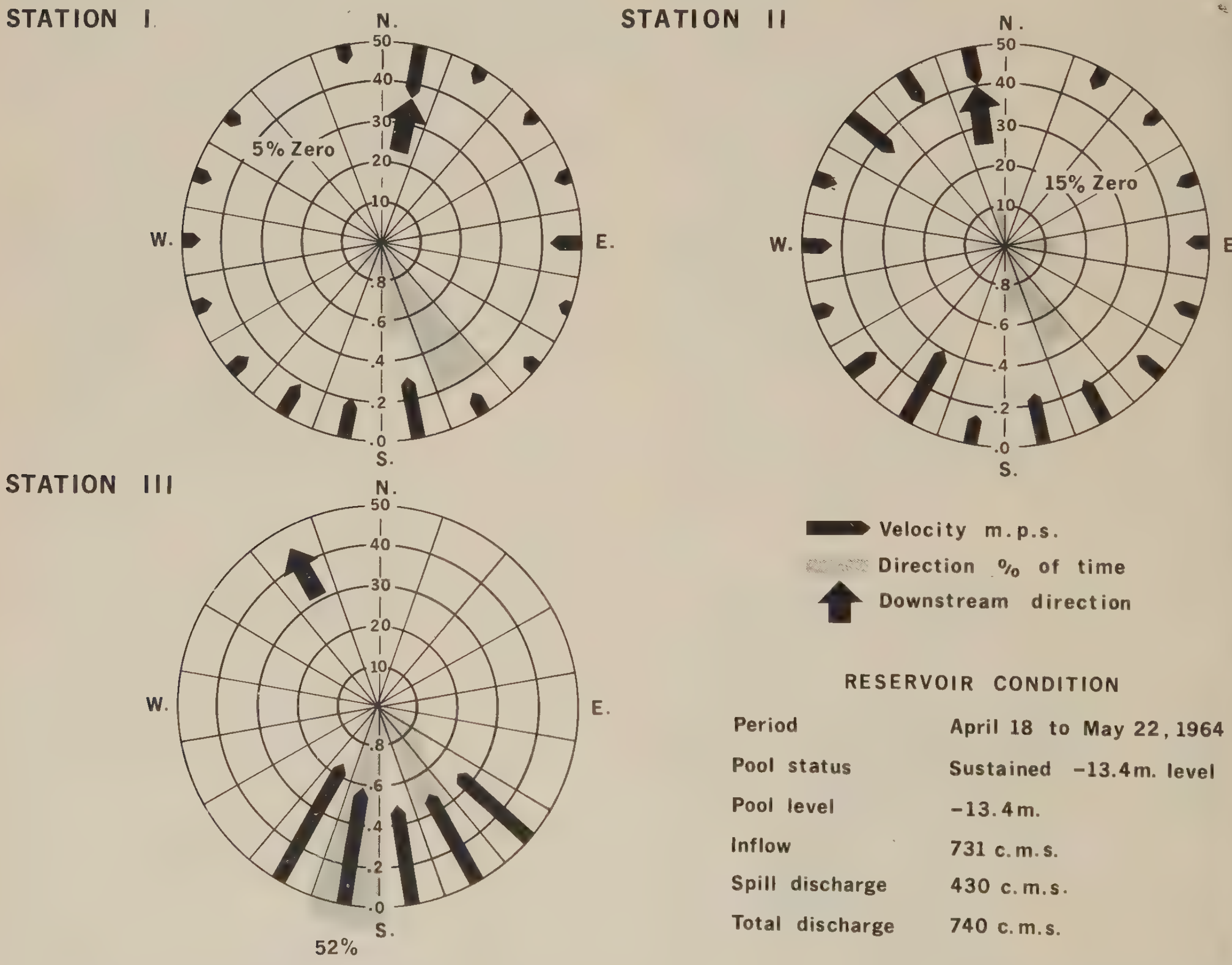
Continuous Current Measurements

The averages (percentages of time) are given for surface current direction and velocity readings (m.p.s.) recorded by continuous current recorders at three midchannel stations (station I—lower reservoir; station II—midreservoir; station III—upper reservoir) during each of five periods. These periods covered the major changes in inflow and outflow and fluctuations of reservoir level from maximum drawdown in March 1964 through fill-up in August 1964—the time of the major fingerling migration through the reservoir. All current meters were maintained at a depth of 3 m.

The terms "downstream," "upstream" (reverse), and "cross reservoir" are used throughout this section of the report to describe direction of currents. Upstream and downstream currents did not deviate more than 60° from the downstream axis; the others were cross currents.

Conditions in the reservoir include maximum drawdown, sustained minus 13.4-m. level with spill, fill-up with no spill, full pool with high spill, and full pool without spill.

Maximum drawdown.—Maximum drawdown (minus 27.1 m.) was on March 18, 1964. The mean



RESERVOIR CONDITION

Period	April 18 to May 22, 1964
Pool status	Sustained -13.4m. level
Pool level	-13.4m.
Inflow	731 c.m.s.
Spill discharge	430 c.m.s.
Total discharge	740 c.m.s.

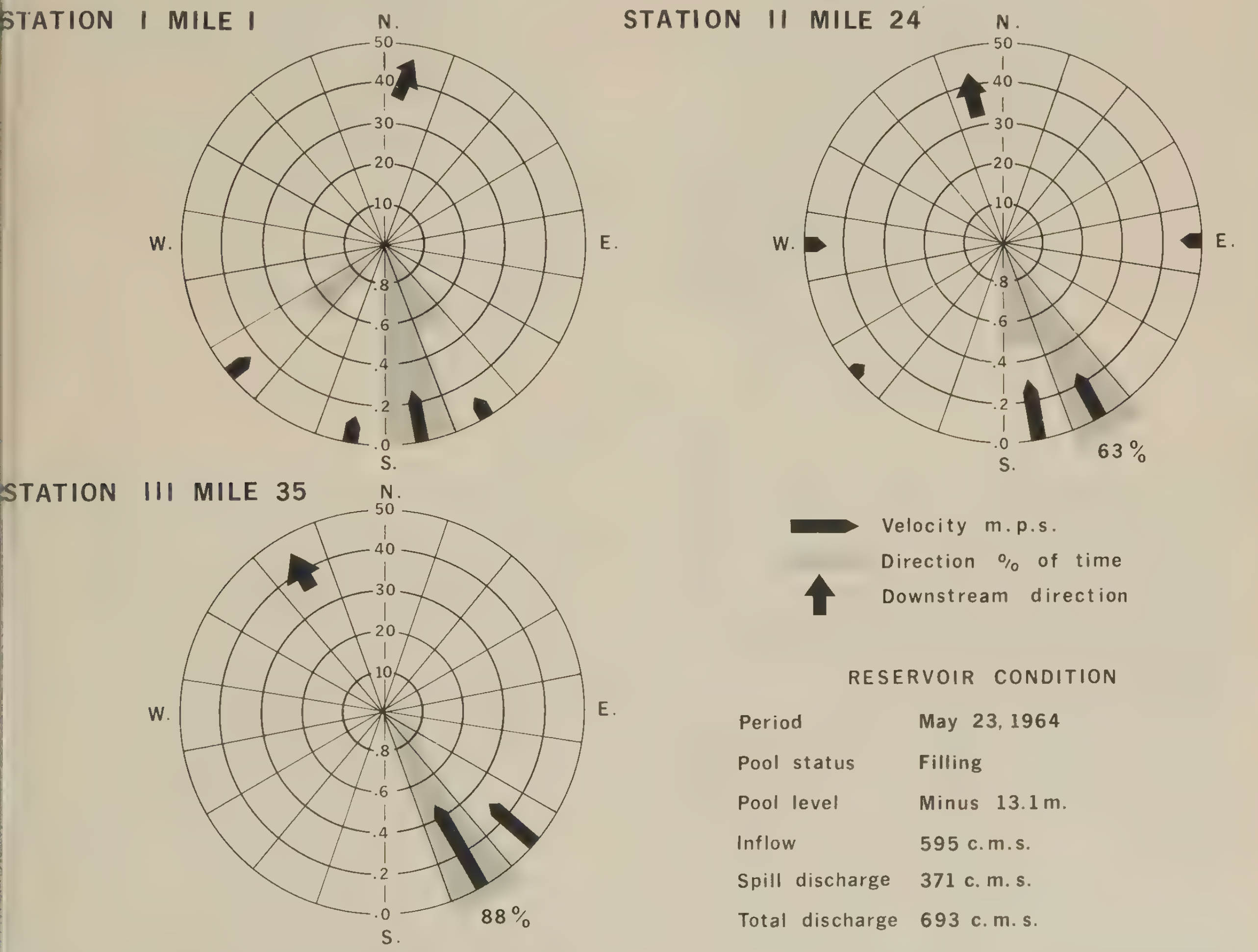
FIGURE 10.—Direction (percentage of time, indicated by scale between center and upper margin of each figure) and average velocity (m.p.s. scale between center and lower margin) of currents recorded at 3-m. depth in Brownlee Reservoir during sustained 13.4-m. level with spill, April 18 to May 22, 1964. Direction of current reads toward point of wedge.

daily outflow (turbine discharge only) from March 13 through April 17 (fig. 9) was 424.4 c.m.s.; the average daily inflow was 511.5 c.m.s. No water was discharged through the spillway. These conditions resulted in gradual filling. Currents were well oriented downstream at stations II and III and reasonably so at station I. Downstream orientation varied from 40 percent in the lower part of the reservoir (station I) to 85 percent in the upper part (station III). Velocities ranged from zero at station I to 0.26 m.p.s. at station III.

Sustained minus 13.4-m. level with spill.—The reservoir was maintained near the minus 13.4-m. level from April 18 through May 22. The average inflow was 731.7 c.m.s., and the mean spillway discharge was 430.4 c.m.s. The rest of the inflow was discharged through the turbines at Brownlee Dam.

The percentage of downstream currents at stations I and III increased considerably over that of the previous period. Downstream orientation increased from 40 to 82.6 percent at station I and from 85 to 100 percent at station III (fig. 10). The percentage of downstream currents at station II decreased from 68 to 49 percent. Some upstream and cross-reservoir currents were also recorded at this station. Velocities ranged from 0.015 m.p.s. at station I to 0.21 m.p.s. at station III.

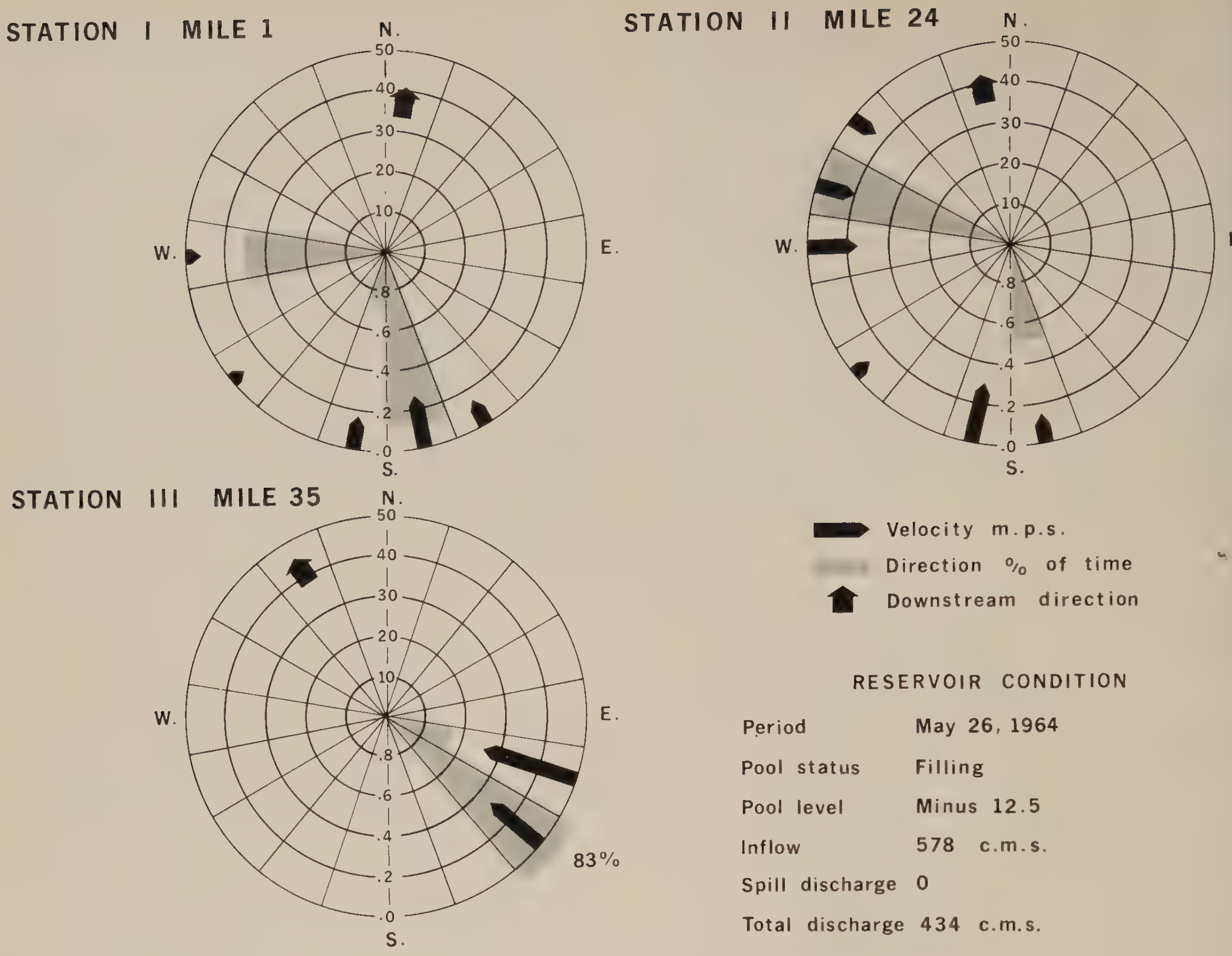
Averages of currents during 3 days separated by 3-day intervals over a period of decreasing discharge in 1964 are compared in figure 11.



RESERVOIR CONDITION

Period	May 23, 1964
Pool status	Filling
Pool level	Minus 13.1 m.
Inflow	595 c.m.s.
Spill discharge	371 c. m. s.
Total discharge	693 c. m. s.

GURE 11.—Direction (percentage of time, indicated by scale between center and upper margin of each figure) and average velocity (m.p.s., scale between center and lower margin) of currents recorded at 3-m. depth in Brownlee Reservoir for three 24-hour periods during rapidly decreasing discharge at the 13.1-m. level (May 23, 26, and 29, 1944). Direction of current reads toward point of wedge.



RESERVOIR CONDITION

Period	May 26, 1964
Pool status	Filling
Pool level	Minus 12.5
Inflow	578 c.m.s.
Spill discharge	0
Total discharge	434 c.m.s.

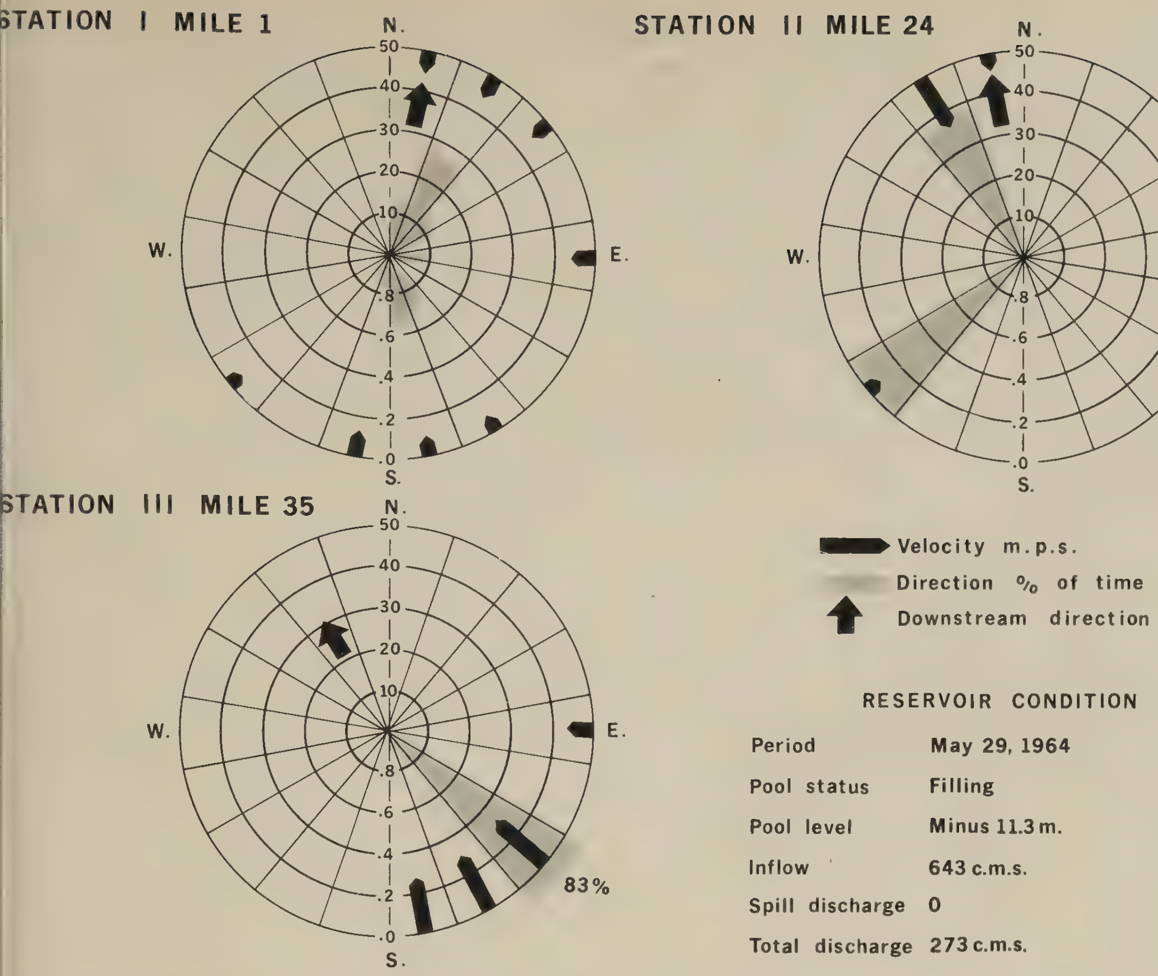
Figure 11.—Continued

The influence of the reduced discharge on currents is readily apparent. On May 23, a day of surface spill and high total discharge, all three stations showed nearly 100-percent downstream orientation of currents. On May 26, the spill was closed and the total discharge was reduced. Current direction at station II shifted from 88 percent downstream to about 58 percent cross reservoir. On May 29, the total discharge was reduced further. A high percentage of the currents at the downstream end and in the middle of the reservoir (stations I and II) were oriented upstream. Downstream orientation of currents at station III shifted slightly; this change may have resulted from the subsequent filling action rather than from the reduced discharge. Currents remained well oriented downstream at station III throughout the period because the reservoir is essentially riverrun in this area at this level.

Fill-up with no spill.—Spilling ceased on May 26, and filling of the reservoir resumed. Figure 12 shows the weekly average current velocities and directions during fill-up from the minus 10.1- to minus 4.9-m. level. Downstream currents decreased at all three stations from those recorded during the previous period (minus 13.1 m.). Upstream currents were about as frequent as downstream currents at station I and II. Currents were still downstream 95 percent of the time at station III. Velocities ranged from zero at station I to 0.17 m.p.s. at station III. Velocity was zero 20 percent of the time at station I.

Full pool with high spill.—The currents from June 13 to 26, when the reservoir was full and a large volume of water was being discharged over the spillway, are described in figure 13.

Currents were weak and downstream orientation was lacking during filling and at full pool im-



RESERVOIR CONDITION

Period	May 29, 1964
Pool status	Filling
Pool level	Minus 11.3 m.
Inflow	643 c.m.s.
Spill discharge	0
Total discharge	273 c.m.s.

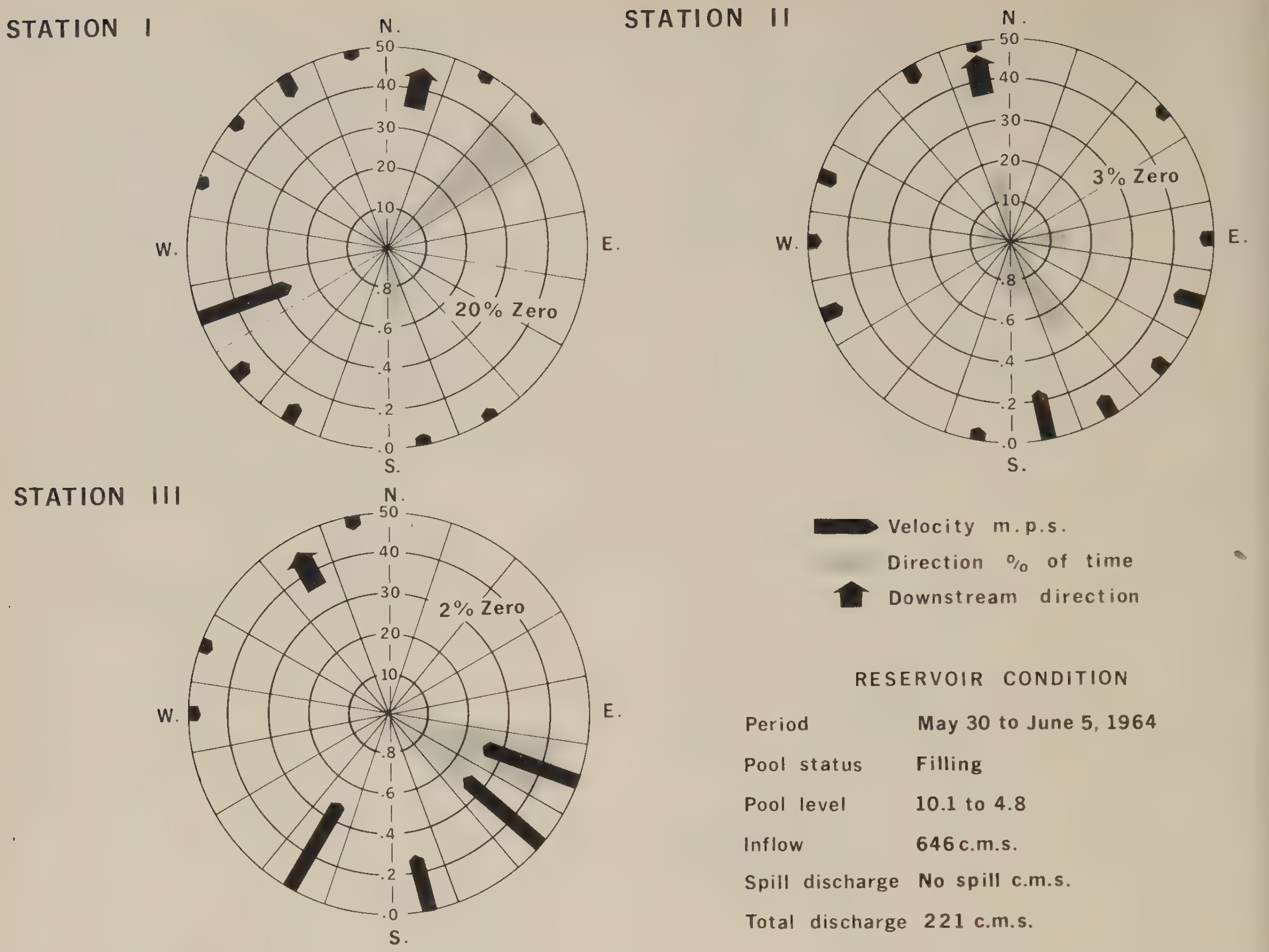
FIGURE 11.—Continued

nediately before spilling (fig. 12). Spilling began again on June 9 and by June 12 had reached bout 708 c.m.s. and through June 13–26 averaged ,013 c.m.s. This spilling caused currents at station I to be oriented downstream; currents were ownstream 93 percent of the time. The percentage f zero readings (66 percent) was high at mideservoir (station II). Currents at the upper end f the reservoir were oriented downstream 49 perent of the time; water velocities here ranged from .07 to 0.18 m.p.s. Vertical and counter currents ndoubtedly accounted for the lack of downstream rientation at the upstream end of the reservoir. Thus, for the period of high inflow and high spill t full pool, currents in the lower reservoir were ell oriented in a downstream direction, but the ischarge had little influence on currents at mideservoir. Velocities increased in the upper reservoir, but downstream orientation of the currents was not visibly stronger.

Full pool without spill.—The reservoir remained at full pool without spill from July 2 to August 25, 1964. The mean daily inflow was 316.2 m.p.s.; the average outflow was 312.3 m.p.s. The reservoir was thermally stratified, and the thermocline was well defined. Downstream movement of surface water was negligible—weak upstream and downstream currents were nearly equal. Current readings of zero were common at midreservoir (fig. 14).

Instantaneous Current Measurements

Instantaneous measurements of current direction and velocity at the limnological stations under the five reservoir conditions are presented. We reasoned that some knowledge of subsurface currents could be gained from these measurements and that



RESERVOIR CONDITION

Period	May 30 to June 5, 1964
Pool status	Filling
Pool level	10.1 to 4.8
Inflow	646 c.m.s.
Spill discharge	No spill c.m.s.
Total discharge	221 c.m.s.

Figure 12.—Direction (percentage of time, indicated by scale between center and upper margin of each figure) and average velocity (m.p.s., scale between center and lower margin) of currents recorded at 3-m. depth in Brownlee Reservoir during filling with no spill, May 30 to June 5, 1964. Direction of current reads toward point of wedge.

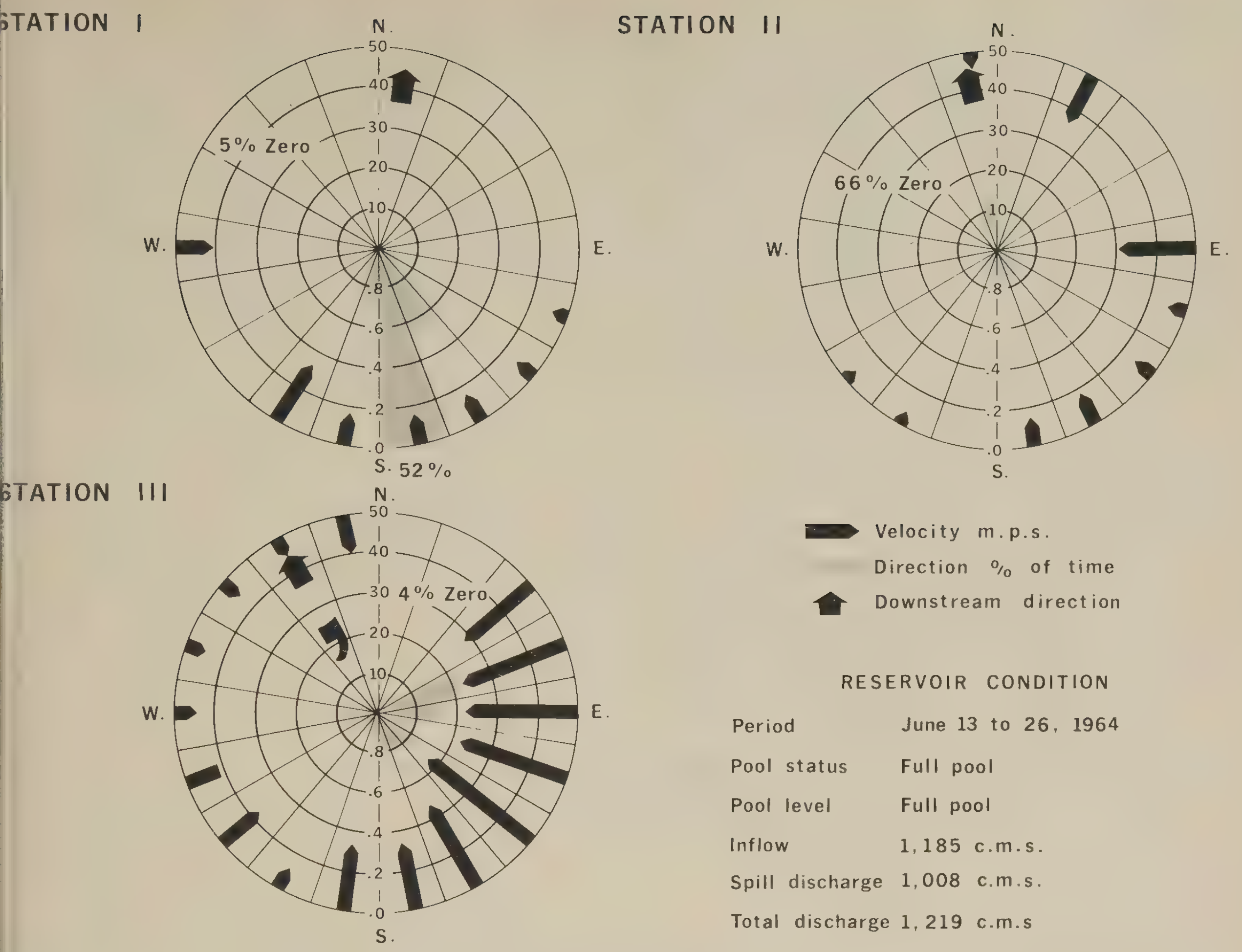
this information might later help us to understand the movement of juvenile salmonids.

As in the continuous current measurements, the instantaneous current measurements were made of maximum drawdown, fill-up with no spill, sustained minus 13.4-m. level with spill, full pool with high spill, and full pool without spill. The effect of wind on the currents was measured also.

Maximum drawdown.—Measurable currents were evident from surface to bottom at most stations throughout the reservoir during maximum drawdown in March 1964 (fig. 15). Velocities varied from 0.08 to 0.51 m.p.s. in the upper end of the reservoir and from 0.00 to 0.15 m.p.s. in the lower end. The direction pattern of surface currents was generally downstream, but some upstream currents were recorded below the surface.

Fill-up with no spill.—Few currents were detectable at the greater depths from station 10 downstream during fill-up in April 1964 at the minus 20.4-m. level (fig. 16). All readings at station 10 (midreservoir) were zero. Temperature data at this time indicated the start of vertical stratification. All readings in the lower end of the reservoir were less than 0.15 m.p.s.

Sustained minus 13.4-m. level with spill.—Velocity and direction were recorded in April at the minus 13.4-m. level when the spillway discharge was about 141.6 c.m.s. and when inflow was about 991.2 c.m.s. This minimal spill and increased inflow



RESERVOIR CONDITION

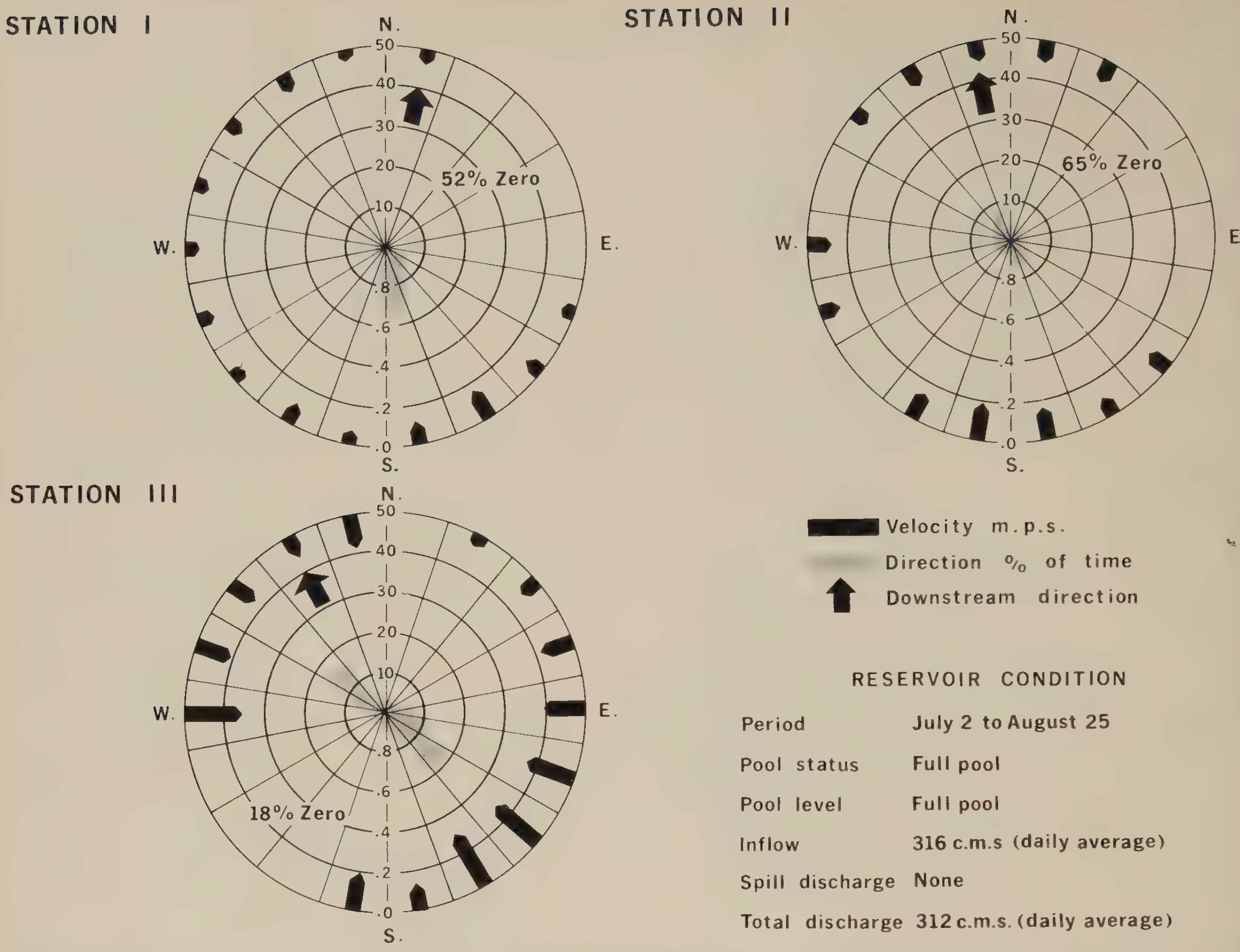
Period	June 13 to 26, 1964
Pool status	Full pool
Pool level	Full pool
Inflow	1,185 c.m.s.
Spill discharge	1,008 c.m.s.
Total discharge	1,219 c.m.s

FIGURE 13.—Direction (percentage of time, indicated by scale between center and upper margin of each figure) and average velocity (m.p.s., scale between center and lower margin) of currents recorded at 3-m. depth in Brownlee Reservoir during full pool with spill, June 13 to 26, 1964. Direction of current reads toward point of wedge.

aused measurable currents at station 10 (fig. 17), vhere readings from top to bottom ranged from .06 m.p.s. to zero. Velocities at the lower end of he reservoir still remained below 0.15 m.p.s. Generally, most currents at the surface were downtream and were measurable from station 20 to the am.

Full pool with high spill.—Instantaneous curent measurements were made again on June 24 nd 25, 1964 (fig. 18), when the reservoir was at ull pool and when the spill was 1,049.1 c.m.s. Curents were measurable from station 20 to the dam rom the surface to 30.5 m. All readings below 8 1 m. were zero in the lower end of the reservoir. elocities in the upper end of the reservoir ranged from 0.04 to 0.30 m.p.s.; in the lower end of the reservoir, velocities ranged from 0.00 to 0.14 m.p.s. The maximum of 0.14 m.p.s. in the lower reservoir was at the 22.9-m. depth at station 6. The direction of currents was generally downstream in the upper levels throughout the reservoir, but some upstream currents were detected in the lower levels at the upstream end.

Full pool without spill.—Instantaneous current measurements at full pool without spill began on July 1 and continued through October 1964. All data were similar to those for August 18 to 20 (fig. 19). Directions of flow at the time of thermal stratification were erratic: velocities rarely exceeded 0.08 m.p.s. even in the upper reservoir



RESERVOIR CONDITION

Period	July 2 to August 25
Pool status	Full pool
Pool level	Full pool
Inflow	316 c.m.s (daily average)
Spill discharge	None
Total discharge	312 c.m.s. (daily average)

FIGURE 14.—Direction (percentage of time, indicated by scale between center and upper margin of each figure) and average velocity (m.p.s. scale between center and lower margin) of currents recorded at 3-m. depth in Brownlee Reservoir during full pool with no spill, July 2 to August 25, 1964. Direction reads toward point of wedge.

(station 20). Velocities and directions of surface currents seemed to depend primarily upon velocities and directions of the wind.

Effect of wind on currents.—The wind near station 14, measured at a set time each day, showed a trend. In contrast, the currents were recorded 24 hours. In future studies of this type, we recommend that wind direction and velocity be measured continuously along with direction and velocity of surface water current at each station so that they can be directly correlated.

Wind direction and velocity had a considerable influence on surface currents. The wind was predominantly northerly or southerly, rarely easterly or westerly (tables 4 and 5). The reservoir flows generally from south to north; thus, the primary effect of wind was either to increase or diminish the velocity of the prevailing surface currents. A wind of high velocity and relatively long duration was required to reverse a prevailing surface current of more than 0.03 m.p.s.

Wind apparently had the least effect near the head of the reservoir, where the inflow had comparatively high velocity during all reservoir stages except at full pool with low inflow. Wind had a decided effect on the lower and middle sections of the reservoir (stations I and II), where velocities rarely exceeded 0.25 f.p.s. (0.08 m.p.s.). Effects were significant at these areas during all reservoir stages except at maximum drawdown. Instantaneous sampling indicated that wind could affect measurable currents to a depth of 8 m.

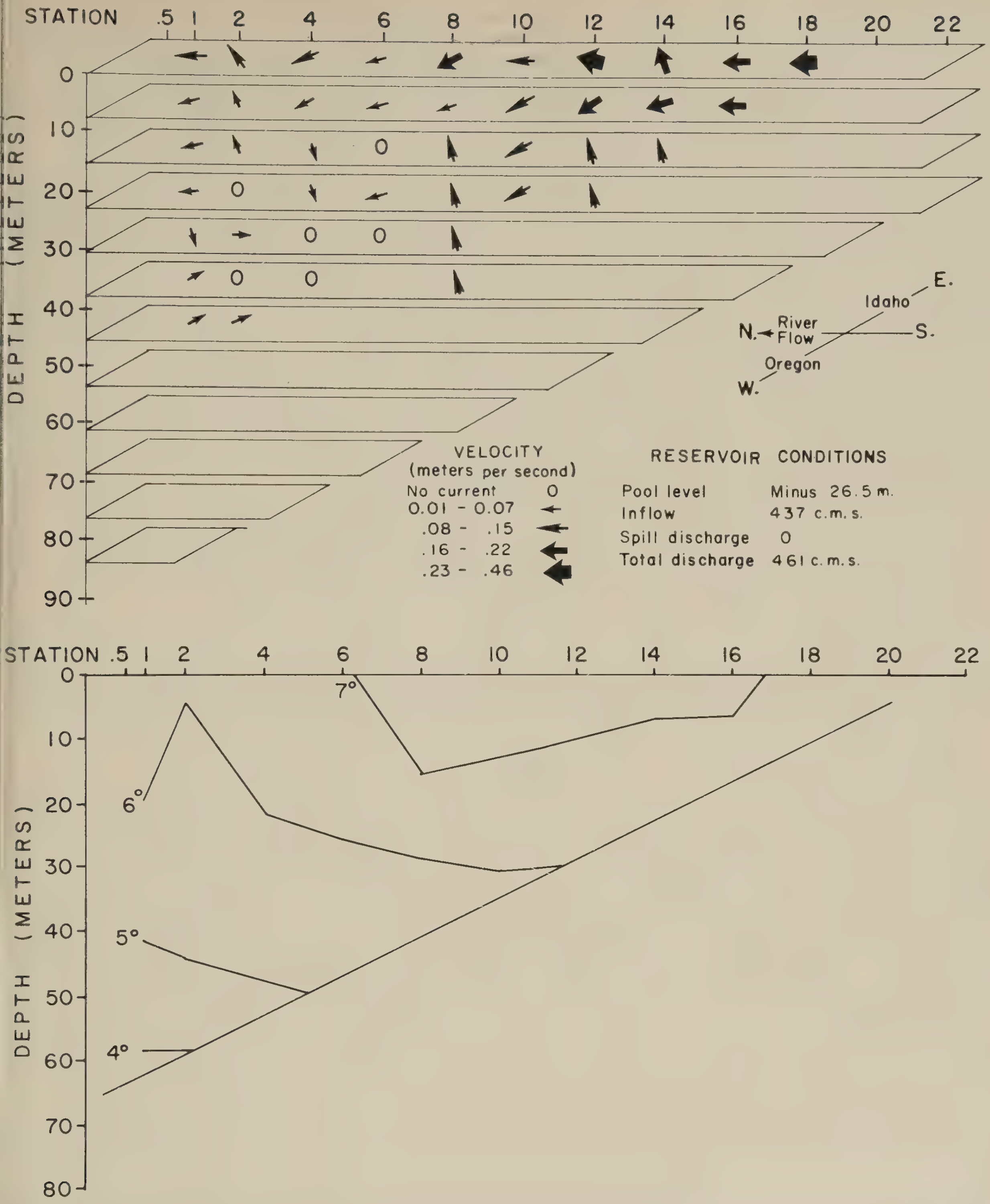


FIGURE 15.—Instantaneous current and temperature readings in Brownlee Reservoir during maximum drawdown, March 23 to 25, 1964.

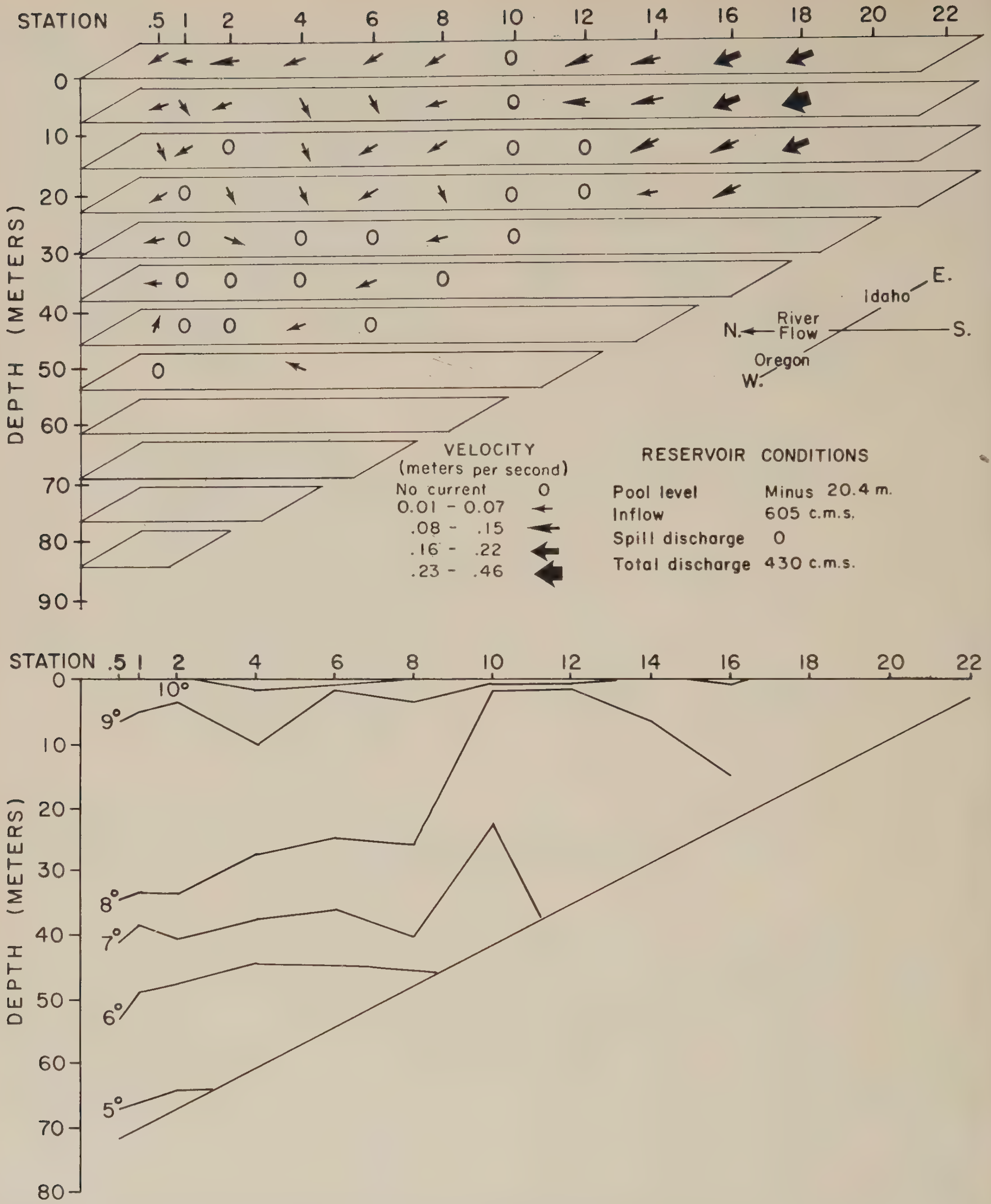


Figure 16.—Instantaneous current and temperature readings in Brownlee Reservoir during filling with pool at minus 20.4 m., April 7 to 10, 1964.

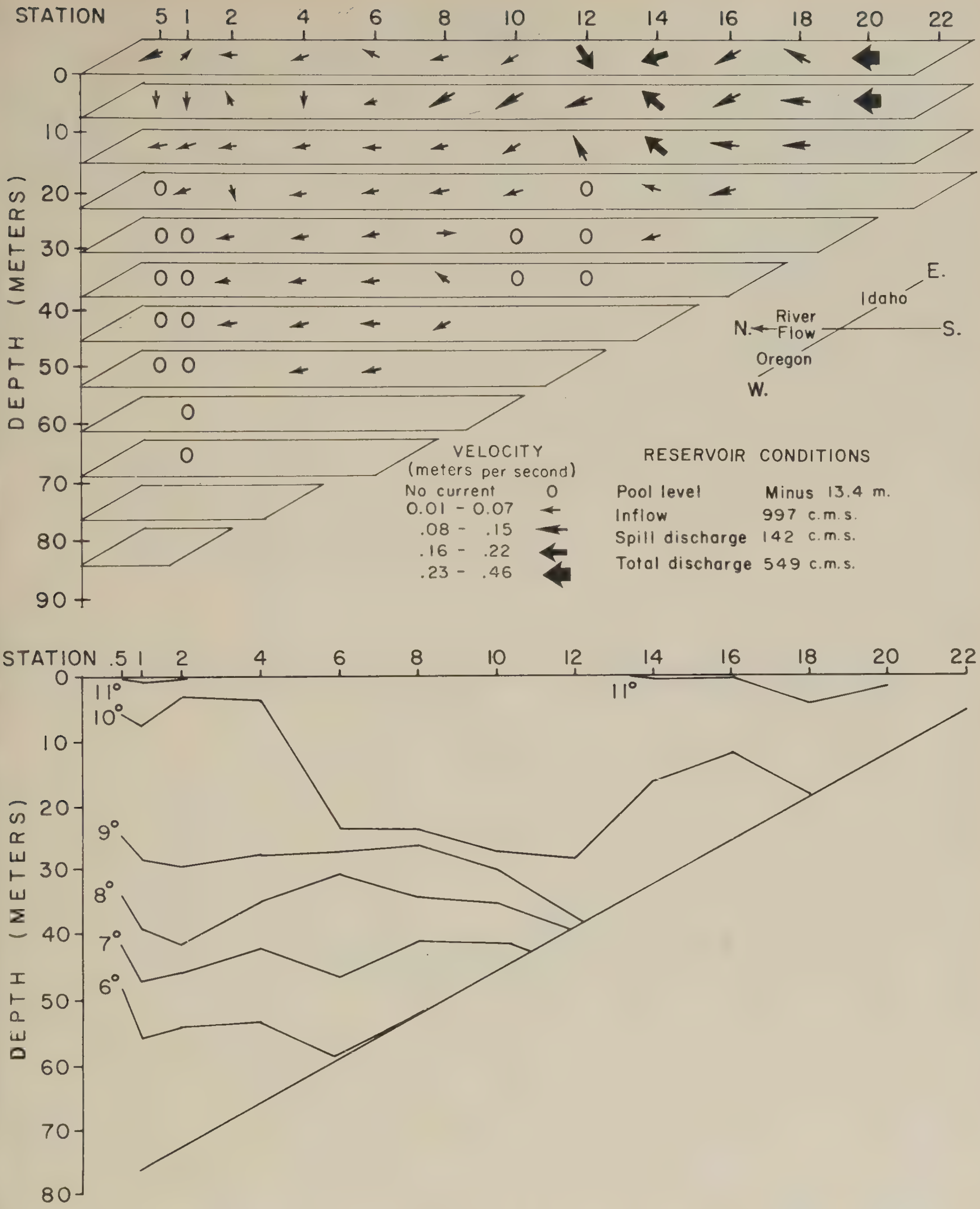


FIGURE 17.—Instantaneous current and temperature readings in Brownlee Reservoir during moderate spilling and with pool level sustained at minus 13.4 m., April 20 to 23, 1964.

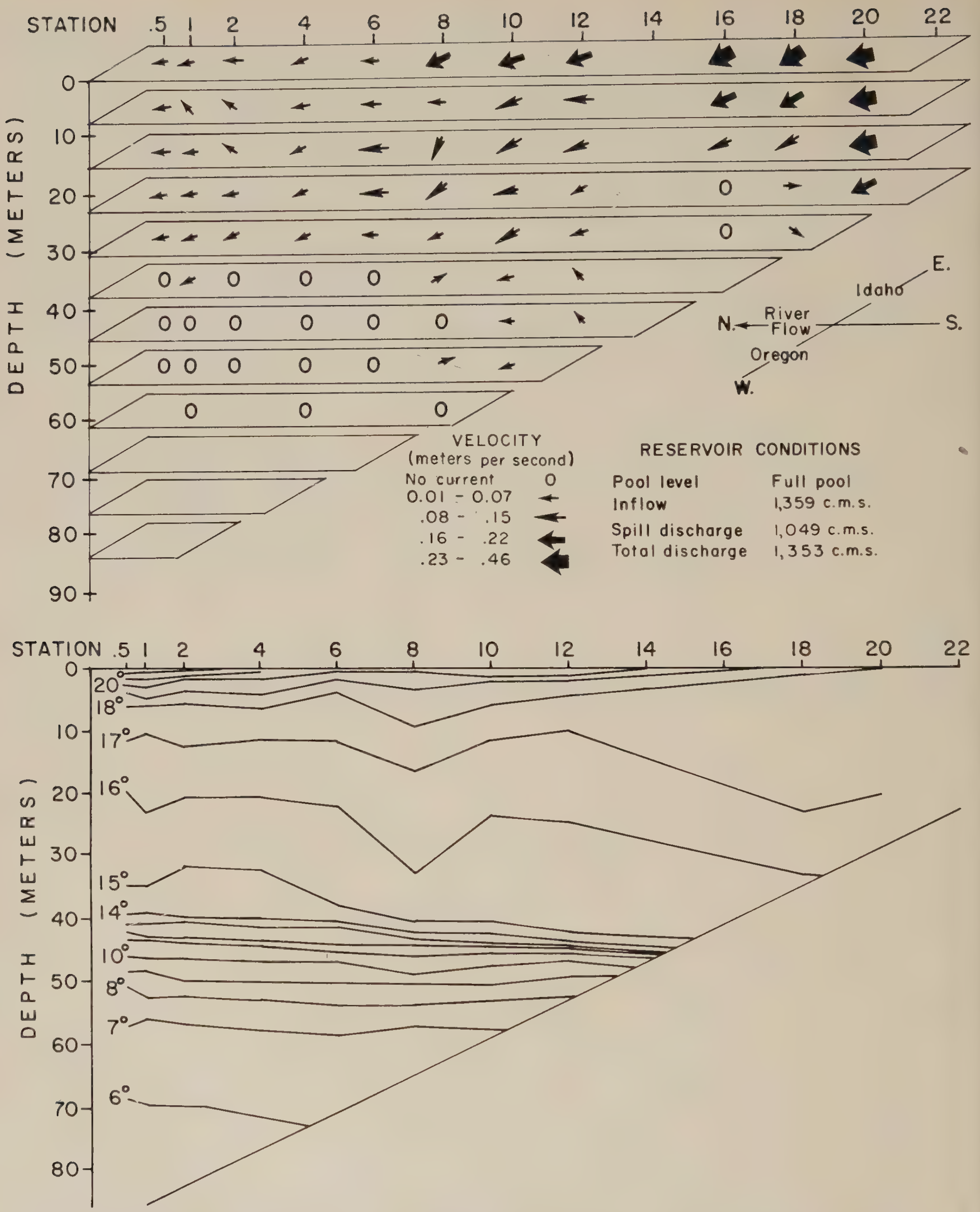


FIGURE 18.—Instantaneous current and temperature readings in Brownlee Reservoir during a heavy spill at full pool, June 24 to 25, 1964.

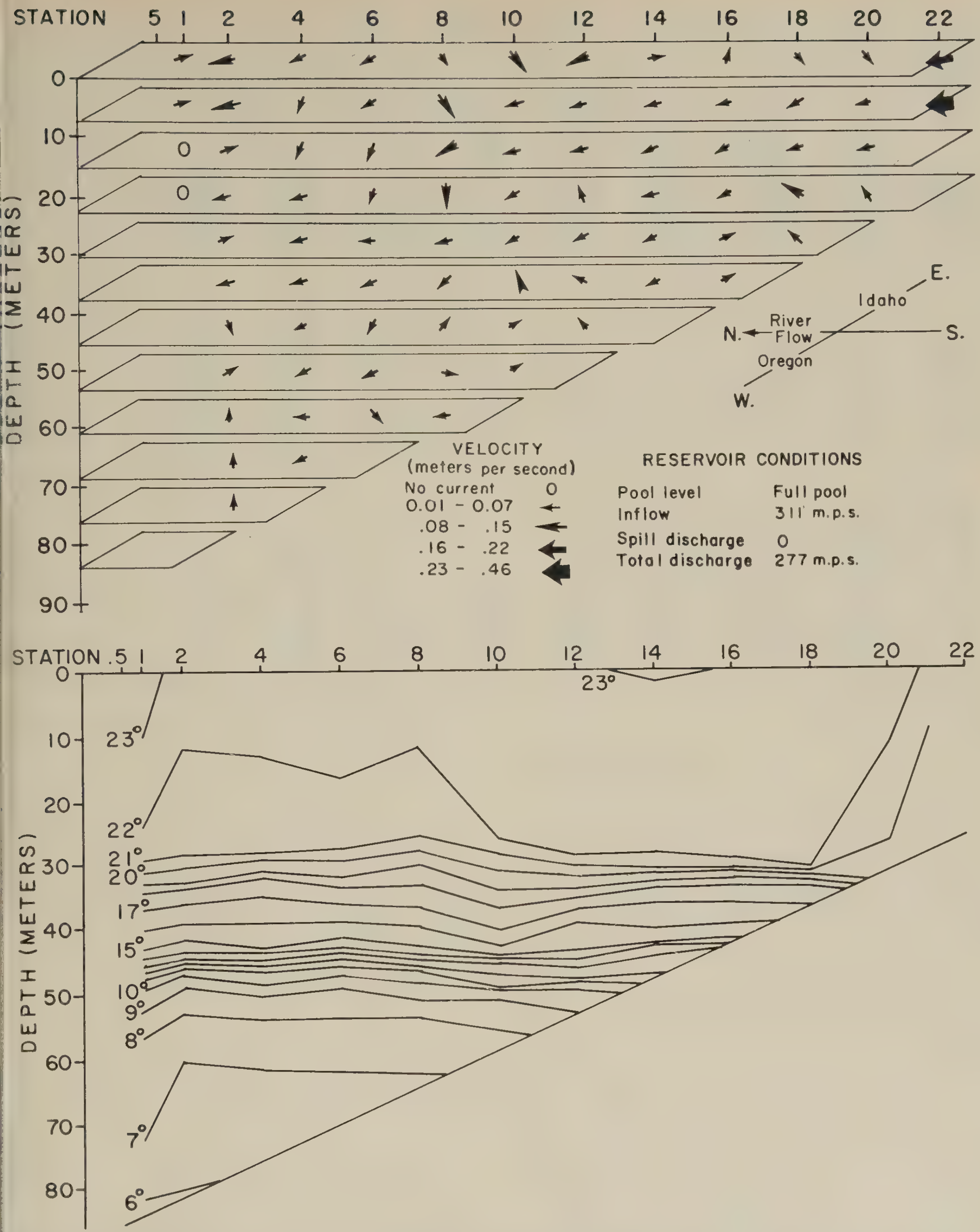


FIGURE 19.—Instantaneous current and temperature readings in Brownlee Reservoir during full pool at no spill and low discharge, August 18 to 20, 1964.

Table 4.—*Prevailing wind direction at station 14 during 5 reservoir stages (determined from single daily observations), March to August 1964*

Reservoir stage	Date	Wind direction		
		North	South	Calm
		Percent		
Maximum drawdown	Mar. 6–Apr. 17	36	25	39
Sustained pool minus, 13.1 m.	Apr. 18–May 22	57	17	26
Fill-up—no spill	May 30–June 5	57	0	43
Full pool—spill	June 13–June 26	50	22	28
Full pool—no spill	July 2–Aug. 25	73	2	25

Factors That Influence Surface Currents

Surface currents are highly important because most of the juvenile salmonids were near the surface upon entry into the reservoir and for some time thereafter. The primary factors that affected surface currents at the three stations were as follows:

Station I (lower reservoir)—rate of discharge and wind
Station II (middle reservoir)—reservoir drawdown, rate of discharge, and wind
Station III (upper reservoir)—reservoir drawdown and rate of river inflow

Surface currents at station I were not well oriented downstream except when the rate of discharge was increased at the spill (figs. 10, 11, and 13). Wind was the main factor affecting currents when there was no spill.

Currents at station II were well oriented downstream during two periods—maximum drawdown at minus 27.1 m. and at the minus 13.4-m. level with spill (figs. 9 and 10). During the rest of the study period, currents at station II were oriented upstream about as often as downstream. The wind again seemed to exert a disorienting influence.

Currents at station III were well oriented downstream except at full pool and at full pool with spill. Although wind seemed to be the most important disorienting factor at full pool, it had less effect on the surface currents at the upper end of the reservoir than at the middle and lower areas. Water velocities at station III were usually in excess of 0.15 m.p.s.; consequently, considerable wind was needed to alter significantly the general downstream current pattern. A wind of high velocity blowing in a reverse direction for a short time might deflect the surface current somewhat, but it would not reverse it.

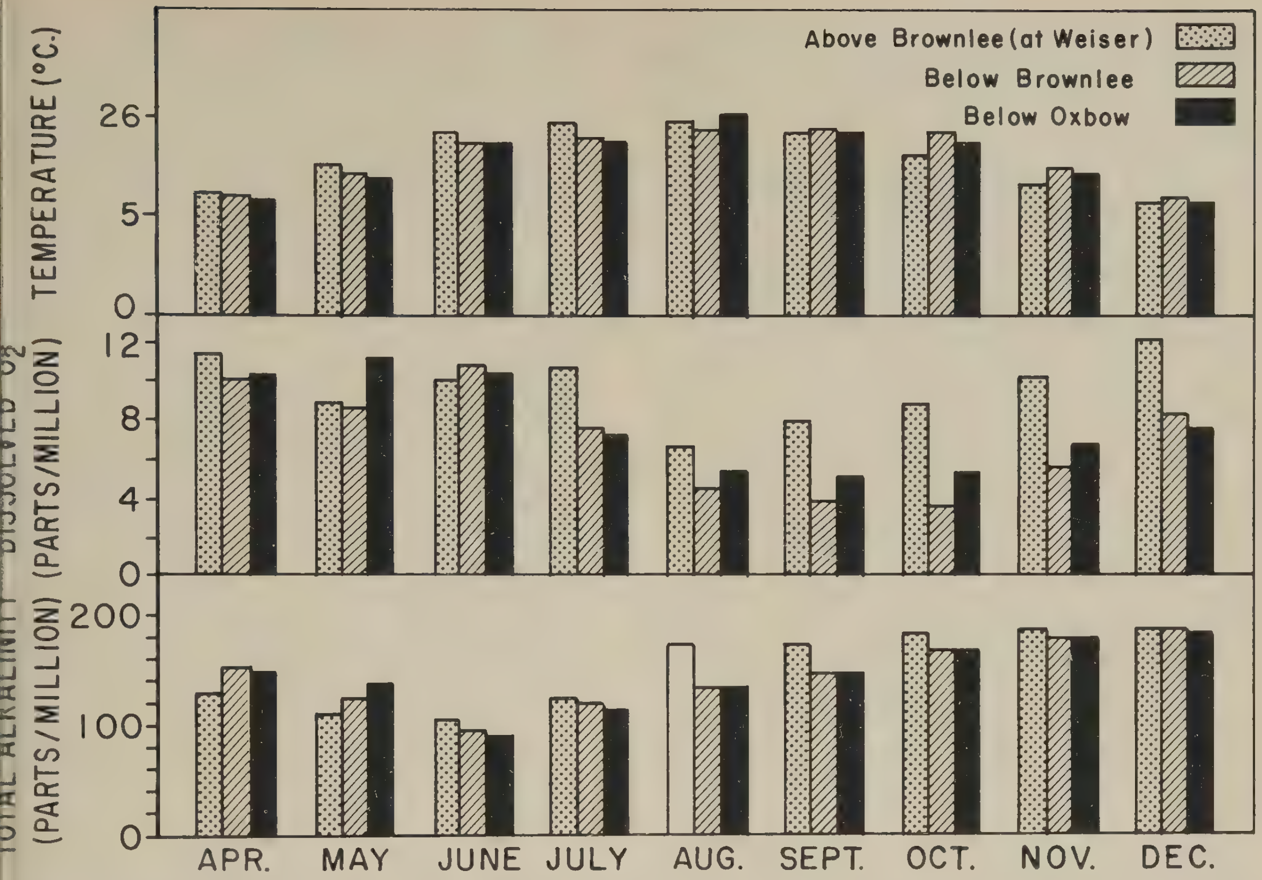
The instability of currents in the upper end of the reservoir during full pool with spill and high river inflow (fig. 13) was probably due to the spill rather than to the wind. Possibly a seiche effect was created during the heavy spill, which caused strong vertical currents near the convergence line. Repeated observations of the movement of the convergence line indicated a definite shift downstream during spilling. When the convergence line moved downstream to the vicinity of the current monitor at station III, the downstream orientation of the current suffered a definite breakdown.

EFFECTS OF BROWNLEE RESERVOIR ON WATER QUALITY OF SNAKE RIVER

Temperature, dissolved oxygen, and total alkalinity were measured in 1963 at three stations along the Snake River: (1) above Brownlee Reservoir (Weiser, Idaho), (2) below Brownlee Dam (interstate bridge), and (3) below Oxbow Dam (powerhouse tailrace). The data are plotted in figure 20 to show the effect of the Brownlee-Oxbow complex on the inflowing river waters from April through December. Upstream from

Table 5.—*Wind velocities and direction recorded during instantaneous current measurements in Brownlee Reservoir, March to August 1964*

Station No.	Dates									
	Mar. 23–25		Apr. 7–10		Apr. 20–23		June 24–25		Aug. 18–20	
	Direction	Velocity	Direction	Velocity	Direction	Velocity	Direction	Velocity	Direction	Velocity
		km.p.h.		*km.p.h.*		*km.p.h.*		*km.p.h.*		*km.p.h.*
0.5			S	8.0	Calm		Calm		NW	6.4– 8.0
1	SE	16.1	S	12.8–14.5	S	8.0–16.1	Calm		SE	9.7–11.3
2	SW	3.2	Calm		S	8.0	Calm		S	9.7–12.8
4	Calm		NE	4.8– 8.0	N	6.4– 8.0	Calm		SE	8.0– 9.7
6	S	9.7	Calm		Calm		S	9.7–12.8	NE	16.1–20.9
8	S		Calm		Calm		S	9.7–12.8	NE	16.1–19.3
10	S	8.0–16.1	S	1.6– 3.2	NW	32.2	S	6.4– 9.7	N	12.8–16.1
12	S	8.0–16.1	SW	3.2– 4.8	NW	8.0–16.1			N	16.1–19.3
14	S	16.1	S	1.6– 3.2	NE	8.0	S	4.8– 8.0	N	6.4– 8.0
16	S	16.1	Calm		SW	3.2– 4.8	S	4.8– 8.0	N	6.4– 9.7
18	S	1.6	NE	16.1–32.2	NE	8.0	Calm		NW	4.8– 6.4
20					Calm		Calm		NW	12.8–16.1
22									W	9.7–12.8



IGURE 20.—Temperature, dissolved oxygen, and alkalinity in the Snake River above Brownlee Reservoir, below the reservoir, and below Oxbow Dam, 1963.

rownlee Reservoir, the Snake River had a rapid icrease in temperature from April through Auust, whereas below Brownlee and Oxbow Dams showed a definite lag in warming. Temperatures ere nearly identical at all three stations in Sepmber. The trend from October through Decemer reversed in the spring and summer; i.e., flowing water cooled rapidly, and outflowing ater was warmer than inflowing water for several onths. Outflow at Oxbow Dam was slightly ooler than that from Brownlee Reservoir; nevereless, it remained warmer than the inflowing nake River water.

Dissolved oxygen concentrations in the river pstream from Brownlee Reservoir remained relively high through July 1963, declined sharply August, and gradually increased in September. uring the same period dissolved oxygen concenrations below Brownlee were much lower than ose in the inflowing water except during heavy spilling discharge in June. Undoubtedly, removal of subsurface water (through turbine intakes) from oxygen-depleted layers in the reservoir caused the lower concentrations of oxygen below Brownlee Dam. Readings fell below 5 p.p.m. from August through October, a condition which approached the critical limit for survival of salmonids (Ellis, 1944), especially when these levels were accompanied by water temperatures in excess of 21.1° C. Oxygen concentrations below Oxbow Dam were somewhat higher; apparently some oxygen was restored in the Oxbow Dam area. Improvement below Brownlee and Oxbow Dam began in November, 2 months after increases in the river above Brownlee.

Measurements of total alkalinity indicated a delay in trends similar to that of temperature and oxygen. In August, the alkalinity of inflowing water increased sharply, whereas the increase in outflowing water was gradual. About 4 months passed before alkalinity below the reservoirs reached that of the inflowing water in August. Again, the delaying effect of the reservoir is apparent.

POSSIBLE EFFECTS OF LIMNOLOGICAL CONDITIONS ON SALMON

The most important environmental factors that could affect the migration, distribution, and survival of juvenile salmonids in Brownlee Reservoir were water temperatures, dissolved oxygen concentrations, and currents.

Temperature tolerance ranges and temperature preferences of juvenile salmon have been determined by several authorities. Brett (1952) listed maximum temperatures for survival of young salmon between 23.8° and 25.1° C. Ferguson (1958) placed the temperature preference for chinook salmon (*Oncorhynchus tshawytscha*) and pink salmon (*O. gorbuscha*) at 11.7° C. Donaldson and Foster (1941) concluded that young sockeye salmon (*O. nerka*) fingerlings were barely able to maintain themselves at 21.1° C. and could not tolerate water as high as 25.5° C. for more than a few days.

Ellis (1944), McKee (1952), and Fisher (1963) discussed dissolved oxygen levels. Ellis stated that dissolved oxygen content of not less than 5 p.p.m. was favorable to a mixed fauna of food and game fish of the "warm water type." McKee indicated that a dissolved oxygen concentration of 3 p.p.m. was minimal for fresh-water fishes. Fisher found that oxygen levels were definitely correlated with growth of coho salmon (*O. kisutch*). In general, high dissolved oxygen concentrations increased growth, and low levels retarded growth.

The temperature and oxygen requirements for salmonids were not always met in Brownlee Reservoir; at times the movement of salmonids was restricted or perhaps seriously impaired. From late July through September, high surface water temperatures and low oxygen concentrations in the hypolimnion limited the survival area to a layer between 15.2 and 30.5 m., where temperatures ranged from 18.3° to 23.9° C. and oxygen fluctuated between 0 and 7 p.p.m. In some zones temperatures ranged from 12.8° to 15.5° C., but these areas were either completely void of oxygen or blocked off by water masses with no oxygen. Thus, horizontal as well as vertical distribution of salmonids was affected by temperature and oxygen. When oxygen blocks were present in the upper reservoir in late July, fish could have been forced up- or down-reservoir by serious oxygen depletion and high temperatures. Growth and survival of individuals remaining in the reservoir during August and September could have been reduced, especially in years when oxygen concentrations were extremely low and temperatures rose to nearly lethal levels. For example, oxygen and temperature were at much more critical levels for salmonids in August 1962 than in August 1963.

Alkalinities, pH, and conductivities were within acceptable limits for fish life, although conductivity and pH reached nearly critical levels at times. Sulfate and alkalinity concentrations during most of the year were suitable if not optimal for aquatic life. McKee and Wolf (1963) stated that the range in concentration of sulfate in U.S. waters that supported good game fish was 11 to 90 p.p.m. They also stated that alkalinity, when caused almost entirely by bicarbonate, did not seem to harm aquatic life. Concentrations of sulfate in Brownlee Reservoir fell within this range, and alkalinity was primarily bicarbonate.

Several authors examined the relations of total dissolved solids, total alkalinity, and conductivity to productivity; most of them found a positive correlation. Northcote and Larkin (1956) indicated, in their study of 100 British Columbia lakes, that total dissolved solids were the most important factor in determining the general level of productivity. Lakes with the highest productivity had total dissolved solids in excess of 100 p.p.m. At the time of one study, the total dissolved solids of Brownlee Reservoir were well in excess of 100 p.p.m. Even though sufficient nutrients were apparently available for high productivity, critical values of temperature and oxygen during midsummer tended to restrict the growth and movement of salmonids in Brownlee Reservoir.

Two of the diurnal studies showed variations in temperature and oxygen concentrations that probably influenced vertical movements of salmonids. Variations in temperature amounted to 1.65° and 2.2° C. in 24-hour periods during July and August 1963, when variations in oxygen concentrations also were significant. Cooling of the surface waters in the evening and early morning may have enabled salmonids to move toward the urface. Oxygen depletion at the lower depths also nay have induced them to move toward the sur- ace.

Diurnal studies in the spring and fall did not how significant variations in either temperature r chemical characteristics of water that might ave noticeably affected the movement or be- avior of fish. In general, the environment in Brownlee Reservoir was suitable for juvenile salmonids in the spring, winter, and late fall, but marginal during the late summer and early fall.

Movements of salmonids were affected by cur- ents during drawdown and periods of increased nflow and outflow. The maximum effect came dur- ng maximum drawdown when current velocities ere highest and direction was strongly oriented ownstream. Laboratory experiments by Gregory nd Fields (1962) indicated that juvenile coho nd chinook salmon showed significant responses o currents with a velocity as low as 0.0039 m.p.s.

Studies at Brownlee Reservoir showed that the irection of water currents significantly influenced ne passage of young salmonids. This finding was ubstantiated by analyses of changes in water cur- ent and subsequent changes in success of passage y juvenile migrants.[3]

The most obvious downstream orientation of urrents was at maximum drawdown, minus 27.1 ., and at minus 13.4 m. at high inflow and out- ow. Conversely, the downstream current was eakest at full pool. Studies by Durkin and Park [4] n rates of movement and by Sims [5] on escapement f juvenile salmonids indicated that passage hrough the reservoir was more successful in the pring of 1964 than in the two previous springs. n 1964, two favorable conditions existed: (1) a airly high river inflow and (2) relatively low eservoir level throughout most of the downstream igration period. Conceivably, then, fingerlings ould have greater success in passing through res- rvoirs of this type if it were possible to create nditions similar to those described without in- icing heavy financial loss to power companies or greatly interfering with water conservation and irrigation practices.

Fall chinook salmon are the most likely of adult migrant salmonids to be affected by the reservoir environment. Water temperatures below Oxbow Dam during peak migration were 2.7° to 4.9° C. higher than corresponding temperatures in the Snake River above the impoundments. At the same time, dissolved oxygen concentrations below Brownlee and Oxbow Dams were considerably lower than concentrations in the inflowing water above these reservoirs. The combination of these two conditions could place additional stress on adult migrants during fall.

SUMMARY AND CONCLUSIONS

Studies of the physical and chemical limnology of Brownlee Reservoir in relation to migrations of salmon began in July 1962 and continued through October 1964. Sampling stations were established throughout the reservoir, above and below the reservoir, and in the main tributaries. Factors studied were water temperature and chemistry, turbidity, weather, river inflow and outflow, and currents.

Temperatures and oxygen concentrations in the spring, late fall, and winter were suitable for salmonids. On the other hand, excessively high epilimnial temperatures (up to 27.2° C.) and dangerously low oxygen concentrations (0–4 p.p.m.) prevailed in August and September. Salmon were forced to occupy a relatively marginal area for survival. Trends in oxygen concentration and temperature in the epilimnial layer of the upper end of the reservoir were significantly influenced either by large volumes of water entering from the Snake River and tributaries or by large discharges at the dam.

A thermocline or metalimnion developed each year. The formation was accompanied by severe oxygen depletion in all areas below the epilimnion. The thermocline was formed fully 2 months earlier in 1963 than in 1962. Time of formation appeared to depend more on the extent of the drawdown and timing of the filling period than on air temperature and volume of water entering the reservoir. A substantial drawdown (minus 12.2 m.) followed by a prolonged filling period delayed formation of the thermocline in 1962, whereas a minimal drawdown (minus 6.1 m.) accompanied with rapid filling accelerated the formation in 1963.

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[3] Durkin, Joseph T., and Donn L. Park. Behavior of juvenile monids in Brownlee Reservoir. Bureau of Commercial Fish- es, Fish-Passage Research Program, Seattle, Wash. [Manu- ipt in preparation.]

[4] See footnote 3.

[5] Sims, Carl W. Escapement of juvenile salmonids from Brown- Reservoir. Bureau of Commercial Fisheries, Fish-Passage Re- rch Program, Seattle, Wash. [Manuscript in preparation.]

An oxygen block appeared in early summer at the upper end of the reservoir in 1962. No distinct block was recorded in 1963, but some oxygen depletion was detected in the same areas.

Changes in temperature and oxygen concentrations were significant during 24-hour sampling periods in July and August. These changes could have influenced diurnal vertical movements of salmonids. Diurnal changes in temperature and oxygen concentrations were not significant during spring and fall.

Carbon dioxide, silicates, sulfates, hydrogen-ion concentration, conductivity, alkalinity, and turbidity were within acceptable limits for fish life, although hydrogen-ion concentrations and conductivity reached nearly critical values at times.

Continuous recordings of surface currents in 1964 indicated that downstream orientation of currents and current velocity changed significantly during five reservoir stages: (1) maximum drawdown, (2) minus 13.4-m. level with high inflow and outflow, (3) fill-up without spill, (4) full pool with heavy spill, and (5) full pool without spill. The conditions of currents for downstream movement of salmonids were best during maximum drawdown and at the minus 13.4-m. level with high inflow and outflow.

Instantaneous measures of current velocity and direction indicated that current velocities increased throughout the reservoir at a maximum drawdown of 27.1 m.; measurable velocities were detected at most depths from the upper to the lower end of the reservoir. Velocities decreased and current directions became erratic during fill-up. Significant spills at the dam increased currents and changed direction of the flow in the upper levels throughout most of the reservoir during April and June 1964.

Wind velocities influenced surface currents in the lower and middle reservoir. The effect of wind was strongest at midreservoir, where current velocities were lowest. A strong wind of 32 km.p.h. or more could reverse the direction of the surface current at all sections of the reservoir.

Brownlee Reservoir significantly affected the temperatures and oxygen concentrations of the Snake River below the reservoir. Temperatures below Brownlee Dam were about 5° C. higher than temperatures in the river above the reservoir during October. Conversely, oxygen concentrations below the dam were 5 p.p.m. lower than in the inflow. These conditions were reversed in June and July. In general, the reservoir had a buffering effect on temperatures, oxygen concentrations, and alkalinity.

The main conclusions bearing on movements of salmon were:

1. Temperatures, oxygen concentrations, and currents are the most critical of the environmental factors that can affect the distribution and survival of salmon in Brownlee Reservoir.

2. Environmental conditions for salmon at Brownlee Reservoir are suitable, if not optimal, in the spring, late fall, and winter. Growth, movement, and survival of resident juvenile salmon during the late summer and early fall can be seriously restricted.

3. Diurnal physical and chemical changes are not sufficient to cause any radical change in the behavior of salmon during the spring and fall. Diurnal variations in the summer, however, can significantly influence vertical movements of salmon within a 24-hour cycle.

4. Surface and subsurface currents are significantly affected by changes in reservoir level and volumes of inflow and outflow. These changes can influence success in passage of juvenile salmon.

5. Brownlee Reservoir alters the water quality of the Snake River below the dam in the spring and fall. These changes are of particular importance to adult fall-run salmon migrants because the reservoir at this time not only delays the cooling cycle of the river but also lowers the oxygen content to nearly critical levels for salmon.

ACKNOWLEDGMENTS

John R. Donaldson, Oregon State University, critically reviewed this paper. The U.S. Department of the Interior Geological Survey and Idaho Power Company provided data on Snake River flows. Donald Montgomery, project leader of this study in 1962, provided the data for that year.

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CHANGES IN ABUNDANCE OF THE GREEN CRAB, *CARCINUS MAENAS* (L.), IN RELATION TO RECENT TEMPERATURE CHANGES

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ABSTRACT

Trap catches, shore surveys, and fishermen's reports lemonstrated that declining abundance of green crabs n northern New England was associated with paricularly cold winters and a cooling trend in the water. Since the mid-1950's, the once great abundance of green crabs in northeastern Maine has declined to a scarcity or total absence. Abundance in southwestern Maine and in Massachusetts has fluctuated widely, nd moderate abundance in Rhode Island decreased onsistently through 1959.

Mass mortalities of green crabs in winter coincided with periods of severe cold. The general abundance and commercial catch of the soft-shell clam (*Mya arenaria*), a common prey of the green crab, increased markedly during the period of decline of the crabs.

Although the decrease in abundance of green crabs is clearly associated with lower temperatures, the relation is not necessarily direct; there are a number of ways in which low temperature, in combination with lowered salinity, low dissolved oxygen, and other unidentified factors, may affect abundance.

The green crab, *Carcinus maenas* (L.), has undergone major changes in abundance and distribution along the northeast Atlantic Coast since the late 1800's. Scattergood (1952) traced the spread of the species northward to Casco Bay in southwestern Maine by the early 1900's, to scattered localities in central Maine by the late 1930's, nd finally into far northeastern Maine and New Brunswick by 1951. He concluded that green crabs, if present at all in northeastern Maine, were scarce in 1939–42. Glude (1955) narrowed the period of greatest increase of green crabs along the Maine Coast to 1948–51 and recorded their spread o Wedgeport, Nova Scotia, by 1954 (fig. 1). The Fisheries Research Board of Canada (1961) reported that the species had extended its range as ar east as Lockeport, Nova Scotia, 64 km. beyond Cape Sable.

The green crab is of minor commercial importance as bait for sport fishermen south of Cape Cod. A limited fishery in Maine, New Hampshire, nd Massachusetts supplies this market.

The major interest in the species in the United States lies in its importance as a predator. Dow nd Wallace (1952) pointed out the significance of the green crab as a predator on the soft-shell clam (*Mya arenaria*). Glude (1955) and MacPhail, Lord, and Dickie (1955) presented evidence to show the seriousness of predation by green crabs on clams in Maine, New Brunswick, and Nova Scotia.

The purposes of this paper are to document changes since the peak of abundance in the mid-1950's and to relate these changes to concurrent changes in temperature.

SOURCES OF INFORMATION

I have used data from three sources: (1) Records of surface sea-water temperature kept at Boothbay Harbor from 1905 through 1967; (2) estimates of the abundance of green crabs and soft-shell clams by biologists, wardens, and fishermen; and (3) quantitative sampling of green crab populations.

RECORDS

Records of surface sea-water temperature were kept at the BCF Biological Laboratory, Boothbay Harbor, Maine, from 1905 through 1967. From 1905 through 1949, thermometer readings were made thrice daily at the station wharf. From 1950 on, instruments have recorded the temperature, sensed at 1.68 m. below mean low water. Infrequent gaps in the recorded data were filled in from temperatures read in flowing water tanks. Daily, monthly, and annual means were derived from the three daily thermometer readings and hourly readings from the recordings. Figure 2 shows the

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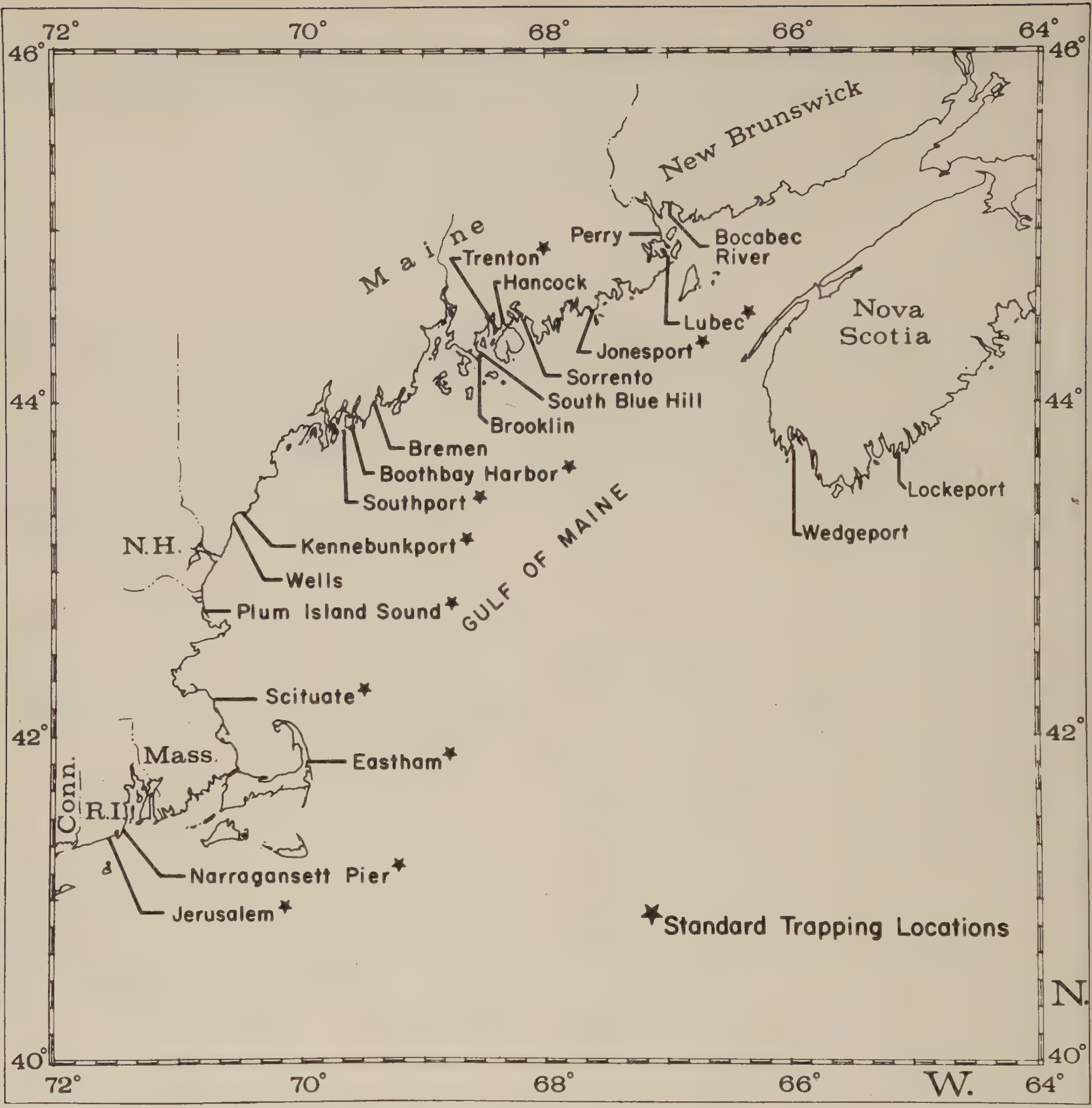
72°
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44°
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40°
New Brunswick
Maine
Perry
Bocabec River
Trenton
Hancock
Lubec
Jonesport
Sorrento
South Blue Hill
Brooklin
Bremen
Boothbay Harbor
Southport
Nova Scotia
Lockeport
Wedgeport
N.H.
Kennebunkport
Wells
GULF OF MAINE
Plum Island Sound
Scituate
Mass.
Eastham
Conn.
R.I.
Narragansett Pier
Jerusalem
Standard Trapping Locations
N.
W.

FIGURE 1.—Location of trapping sites and other areas mentioned in text.

annual means and means for the coldest month of each year.

ESTIMATES

Estimates of the abundance of green crabs and soft-shell clams from the early 1920's to 1951 were obtained from two sources. First, F. E. Goucher, the Clam Commissioner of Essex, Mass., who dug clams for over 22 years, wrote of his own and other fishermen's observations in northern Massachusetts.[1] Second, about 100 coastal wardens and fishermen were interviewed in cooperation with the Maine Department of Sea and Shore Fisheries. Their recollections applied to Maine, but the information reported for southwestern Maine agreed well with that of Goucher (see footnote 1) for northern Massachusetts.

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[1] Goucher, Franklyn E. 1951. Commentary of a clam digger. Unpublished manuscript on file at the BCF Biological Laboratory, Boothbay Harbor, Maine.

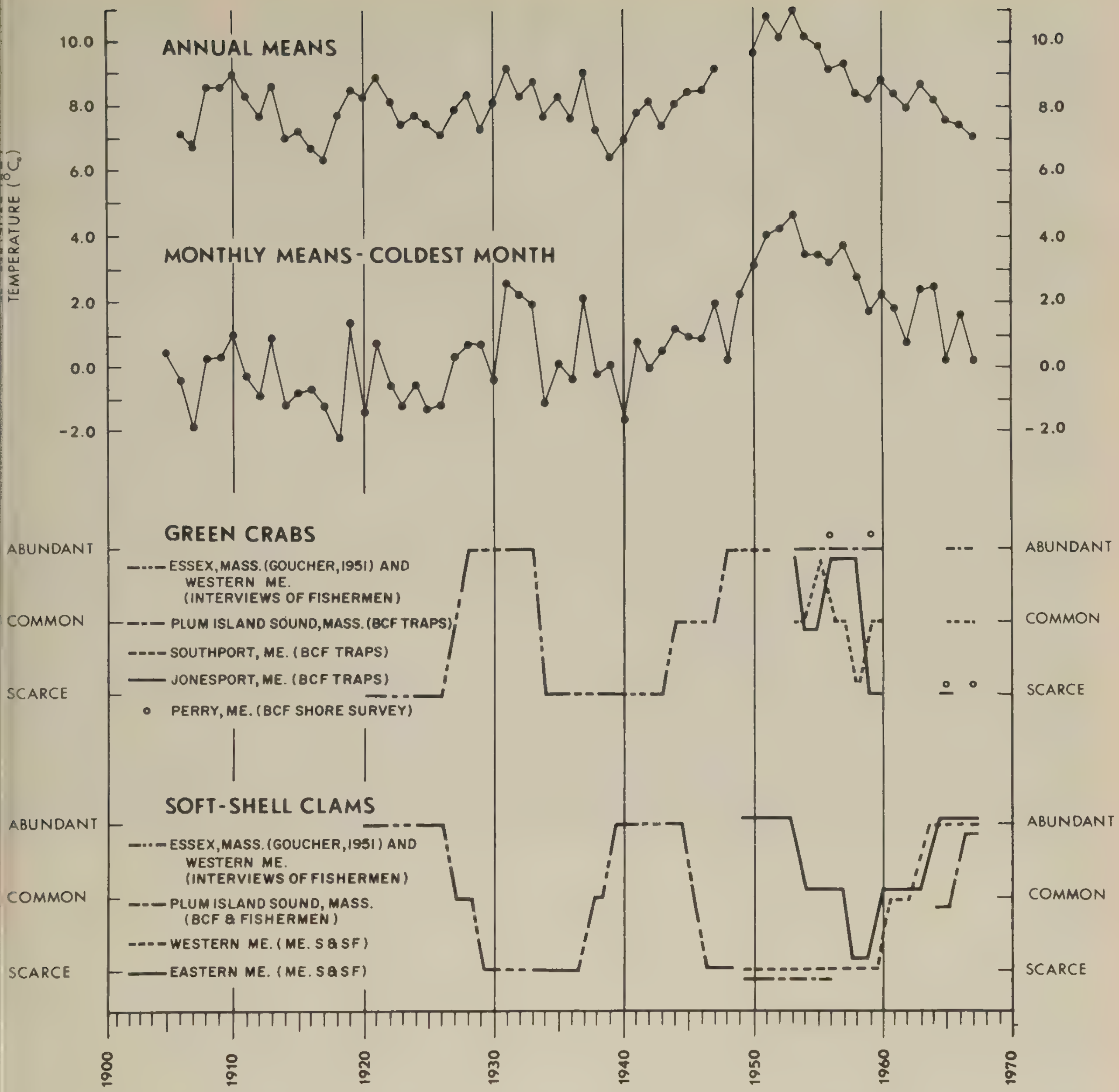

FIGURE 2.—Comparison of annual mean temperatures and lowest monthly mean temperature for each of the years 1905–67, with the abundances of green crabs and soft-shell clams. Equal levels of abundance occurring at the same time and place are shown as slightly displaced lines.

Estimates of the abundance of clams from 1949 through 1967 were furnished by biologists of the Maine Department of Sea and Shore Fisheries.

QUANTITATIVE SAMPLING

BCF biologists used standardized methods to trap crabs in various locations from 1953 through 1960 and 1965 through 1967. The specially designed traps (fig. 3) were built to the same dimensions, were baited with 4.5 kg. of fresh or frozen herring each day, and were fished at the same locations in the same depth of water each time. The traps were fished for 24 hours on 2 consecutive days during the first week of each month from late spring to late fall, when the crabs were most active. The catch and old bait were removed each day. The crabs were sexed, counted, measured, and destroyed. The catch per trap per day, used

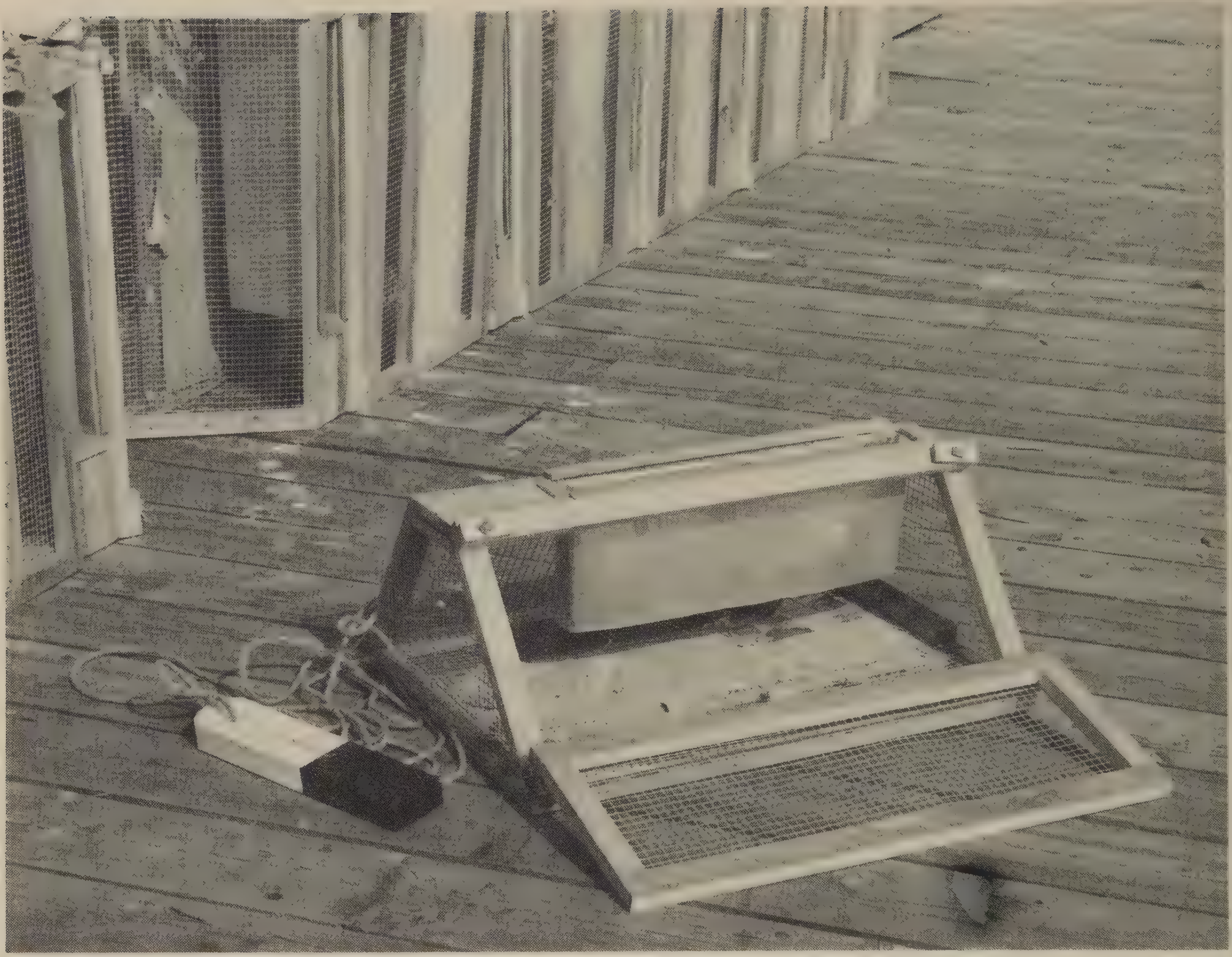

FIGURE 3.—Standard trap used for sampling green crab populations. The deep, sheet-metal funnel prevents escape. The outside dimensions are 81 cm. long by 61 cm. wide by 34 cm. high.

as a measure of abundance, was calculated for each month and each location.

Occasional shore surveys in the intertidal zone supplemented trap catches. The surveys were at low tide in widely scattered areas where traps were not being fished and where there was good to excellent cover for crabs. During a timed search, requiring at least 1 man-hour of effort, all crabs that could be found in the open, under seaweed or stones, or in burrows, were collected, sexed, counted, and measured. Abundance was expressed as the number of crabs found per man-hour of effort expended.

CHANGES IN ABUNDANCE OF GREEN CRABS

In 1953–67 green crab populations were sampled to detect major changes in abundance. Because the month of maximum catch varied from year to year and place to place, I have used only the maximum monthly mean catch per trap per day for each year when comparing years and areas (fig. 4). Individual trap catches at any location during one monthly trapping period (3 traps for 2 days, or 6 catches) showed an average variation of ±15 percent around the mean, with an extreme of ±40 percent. This degree of variability in catch limits the quantitative value of the trapping surveys, but the trends were consistent with general observations and the results of the shore surveys.

The possibility of reducing crab populations by trapping was tested by fishing 18 traps daily for 36 consecutive days in a 5.7-hectare (14-acre) cove. A total of 33,760 crabs was removed at an average catch rate of 52 crabs per trap per day, but there was no significant reduction in numbers by the

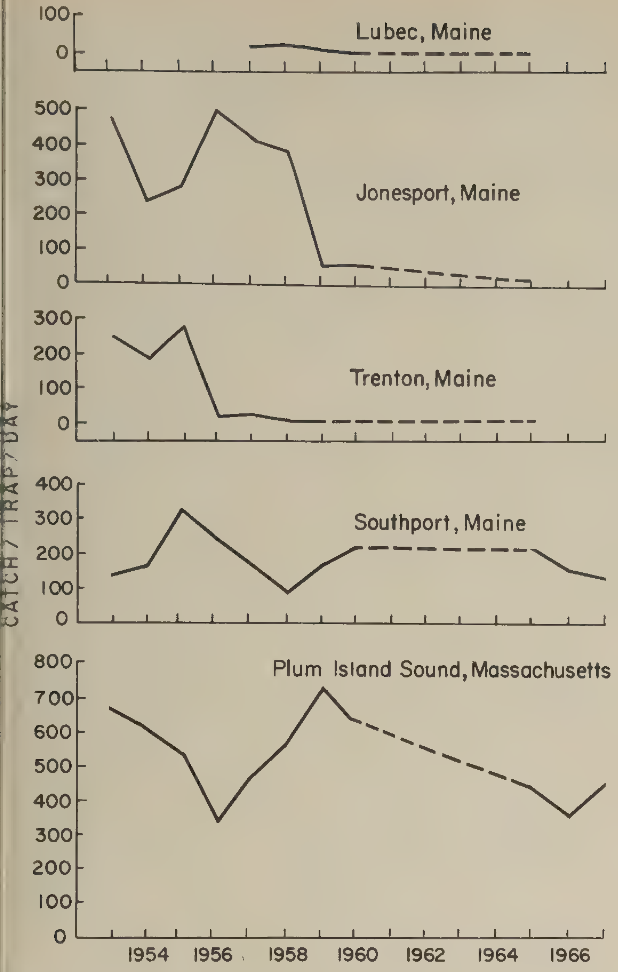

Figure 4.—Greatest monthly mean catch of green crabs per trap per day in each year, 1953–67. Locations are arranged from northeast (top) to southwest (bottom). Broken lines indicate periods when no trapping was done.

end of the period. In Canada, MacPhail et al. (1955) fished two traps daily for 24 days and removed 14,915 crabs without a drop in catch. It appears that, in areas where crabs are generally abundant, they move about sufficiently to fill any gap temporarily caused by trapping.

The most radical changes in abundance have been in Canada and northeastern Maine. During the summer of 1954, MacPhail et al. (1955) trapped an average of 343 crabs per trap per day for 24 days in a rocky area of the Bocabec River in New Brunswick, Canada. Soon after 1954 the green crab population started a continuous decline; the catch per trap dropped to 53 in 1958, 41 in 1959, and 7½ in 1960 (Fisheries Research Board of Canada, 1961).

In Perry, Maine, on Passamaquoddy Bay, shore surveys yielded 552 crabs per man-hour in August 1956 but only 7 per man-hour in September 1965. At nearby Lubec, where trapping was not started until 1957, maximum monthly catches were 13 and 16 crabs per trap per day in 1957 and 1958, but dropped to zero by 1960 and were still zero in 1965.

Trap catches at Cummins Beach, Jonesport, Maine, ranged between 235 and 500 crabs per trap per day in 1953–58, dropped to 50 in both 1959 and 1960, and to 6 in 1965. Shore surveys made in September 1965 at two locations near Jonesport yielded 3 and 11 crabs per man-hour.

In Trenton, Maine, at the Mount Desert Island bridge, where trapping began in 1953, catches dropped abruptly from a maximum of 271 crabs per trap per day in 1955 to 5 and 8 in 1956 and 1957. Catches then dropped to zero in 1958 and were still zero in 1965. A shore survey in nearby Sorrento yielded 14 crabs per man-hour in September 1965.

Trap catches have fluctuated in 1953–67 at Southport in central Maine and Plum Island Sound in northern Massachusetts; and over shorter periods in Boothbay Harbor and Kennebunkport, Maine, and in Scituate and Eastham, Mass. None of these fluctuations have reached points as low as those given above for northeastern Maine and Canada.

Two locations in Rhode Island showed a more gradual but consistent decline of crabs over several years. At Narrow River in Narragansett Pier maximum monthly means dropped steadily from 127 crabs per trap per day in 1956 to 51 in 1959. At Potter Pond Outlet in Jerusalem the means dropped from 334 in 1955 to 88 in 1959. The abundance in later years was not determined.

CHANGES IN WATER TEMPERATURE

The trend in coastal sea-water temperature has changed markedly since the early 1950's when the importance of the green crab was first being realized in northern New England. I have shown (Welch, 1967) that the peak of warming of surface sea water at Boothbay Harbor, Maine, since 1905 was in 1953 (annual mean, 11.1° C.); that the subsequent trend has been toward lower temperature (1967 annual mean, 7.3° C.); and that, although both summer and winter temperatures have followed the same downward trend as the annual means, the decreases have been greater during the winters. Lauzier (1965) has shown that air and sea temperature trends similar to those recorded at Boothbay Harbor have occurred at various points along the western north Atlantic Coast from Atlantic City, N.J., to Halifax, Nova Scotia, and stations over the Scotian Shelf. The sea temperature trend at St. Andrews, New Brunswick, is of particular interest because the station is on Passamaquoddy Bay, a part of the Bay of Fundy where observations were made on crab abundance, and because the general trend is similar to that at Boothbay Harbor. The peak of the warming period at St. Andrews was in 1951, and the temperature declined rapidly after 1954.

RELATION OF CRAB ABUNDANCE TO TEMPERATURE CHANGE

Past records in different areas have indicated that the green crab suffers from extreme or sudden decreases in temperature and apparently prospers in periods of increasing temperature. Broekhuysen (1936), working near Den Helder, Netherlands, found that the development of the eggs of this species was most successful within an optimum range of water temperature and salinity and that a combination of low temperature and low salinity adversely affected egg development and probably the development of adults as well.

Glude (1955) associated increases in green crab abundance with the increase in sea-water temperature—especially winter temperature—and speculated on ways in which temperature could affect the crabs. He also pointed out that Goucher (see footnote 1) had recorded an increase in green crabs at Essex, Mass., between 1926 and 1933 (a period of warming); an abrupt decrease of crabs after the very severe winter of 1933–34; and an increase in abundance again from 1944 to 1951, coincident with the most recent warming period.

Taylor, Bigelow, and Graham (1957) discussed the changes in distribution and abundance of numerous marine animals during the period when information on abundance and temperature has been available. They mentioned that too little was known about the life history of the green crab to say what environmental factors affected it so favorably, but that the winter temperatures of the mid-1950's seemed sufficiently high to account for the northward extension of its range.

Waugh (1964) and Crisp (1964), investigating the effects of the severe winter of 1962–63 on marine life in southern England and North Wales, respectively, found heavy mortality among adult green crabs, but smaller individuals seemed less affected. During most of January and February 1963 the water temperature was about 5° C. below normal, often reaching well below 0° C.

Along the Maine Coast, the most drastic and noticeable decreases in crab abundance were during the winter of 1955–56. Mean monthly water temperatures at Boothbay Harbor for December 1955 (4.9° C.) and January 1956 (3.4° C.) were the coldest in 8 years. These conditions occurred at a time when crab abundance was near an alltime high and when fishermen and others had been alerted to the threat of the green crab. Throughout 1956, I received numerous reports attesting to a decrease in the numbers of crabs seen along the shore or taken in lobster traps during the summer. Of greatest interest were the reports of dead crabs during the winter.

On the Skillings River, in Hancock, Maine, clam diggers observed that green crabs became very active during a thaw in January and were out in the open on the clam flats. The temperature dropped suddenly, and shortly thereafter many dead crabs were found along the shores. This area is near the trapping location at Trenton, where catches dropped sharply from 1955 to 1956.

A lobsterman reported that when the ice broke up in Blue Hill Bay in 1956 he saw large numbers of green crabs washed up along the South Blue Hill shore.

Another lobsterman reported many dead green crabs during the winter of 1955–56 at Herrick Bay in Brooklin, Maine. During the following summer, he found the crabs far less numerous in his lobster traps there.

At Sams Cove, Bremen, Maine, in January 1956, BCF biologists saw hundreds of dead and dying green crabs on muddy bottom at 0.3 to 1.2 m. below mean low water. Heavy ice cover prevented us from examining much of the bottom, but we found crabs lying on the bottom at a time when they would normally be buried. We do not know when the conditions occurred that killed the crabs nor do we know what those conditions were. A few days after the crabs were found, temperature, salinity, and dissolved oxygen in the water between the ice cover and bottom were within the normal range for green crabs. Winter mortality was sufficiently heavy to reduce trapping and shore collections during the following summer to about one-tenth the catches of the previous year.

During the winter of 1958–59 BCF biologists observed another winter kill in southwestern Maine. Monthly mean water temperatures from January through March 1959 were the lowest for all 3 months since 1948. Monthly mean air temperatures for December and February were the lowest for those months since 1917 and 1934, respectively (U.S. Environmental Science Services Administration, 1967). In the tidal marshes in Wells, where many crabs overwinter intertidally in burrows in banks of *Spartina* sod, we found hundreds of dead crabs of both sexes and all sizes. Trap catches in the marshes during the 1959 season were much smaller than in previous years, and the proportion of small crabs in the catch was much higher. This last observation seems to confirm Waugh's (1964) and Crisp's (1964) observations that the smaller individuals of the species suffer less from the effects of low temperature than do the larger ones.

CONCURRENT CHANGES IN CLAM ABUNDANCE

Although the primary purpose of this paper is to report on changes in green crab abundance, the importance of the species as a clam predator justifies mention of changes that have taken place in Maine soft-shell clam stocks as a result of decreased predation. Glude (1955) demonstrated correlations among the increase of green crabs, the decrease of soft-shell clams, and the increase in water and air temperatures. Because of the overwhelming abundance of crabs, he predicted a bleak future for the clam industry if the weather continued mild.

During clam population surveys in the period of heavy predation, BCF biologists consistently found evidence of adequate annual sets of clams; however, each year class was regularly destroyed as the individual clams became large enough for the crabs to find. Nevertheless, the reproductive potential existed for the recovery of clam stocks at any time when predation either decreased naturally or was controlled by man.

The decreasing abundance of crabs during the late 1950's caused a lessening in the effects of predation on the clams and resulted in an increasing supply of clams. Catches of clams have improved markedly in recent years in the two southwestern counties of Maine and to a lesser extent in the rest of the State (fig. 5). In the northeastern counties, where the decrease in crabs has been most pronounced, catches have also increased, but to a far less extent because of an unfavorable market. Reports from clam diggers, coastal wardens, and the resident State biologist, have indicated that clam flats in the northeastern area are well populated with market-size clams (fig. 2). During the course of the crab surveys, I have confirmed these reports by sampling a number of clam flats. Year classes of the past 3 to 5 years were represented consistently in the samples, and usually sufficient market-size clams were present to make clam digging worthwhile.

SUMMARY OF EFFECTS OF TEMPERATURE ON ABUNDANCE OF GREEN CRABS

Carcinus maenas is markedly affected by temperature changes. Documentation is sufficient to show that mass mortalities are often associated with unusually cold winters and that widespread increases and decreases in abundance are associated with long-term warming and cooling trends.

The direct correlation of abundance of green crabs with water temperature and the inverse correlation of abundance of clams with abundance of crabs is compared in figure 2. The close relation of the very low February temperatures of 1934 to the scarcity of crabs later in the same year as observed by Goucher (see footnote 1), and the ensuing increase in the number of clams is especially notable.

There are many ways in which this crab may be favorably affected by higher temperature, either directly or indirectly. Scattergood (1952) pointed out that numerous means have long been available to aid in the spread of the green crab northward—for example, the transportation of larvae by ocean currents, or of adults in fish and lobster shipments. Survival and successful reproduction did not

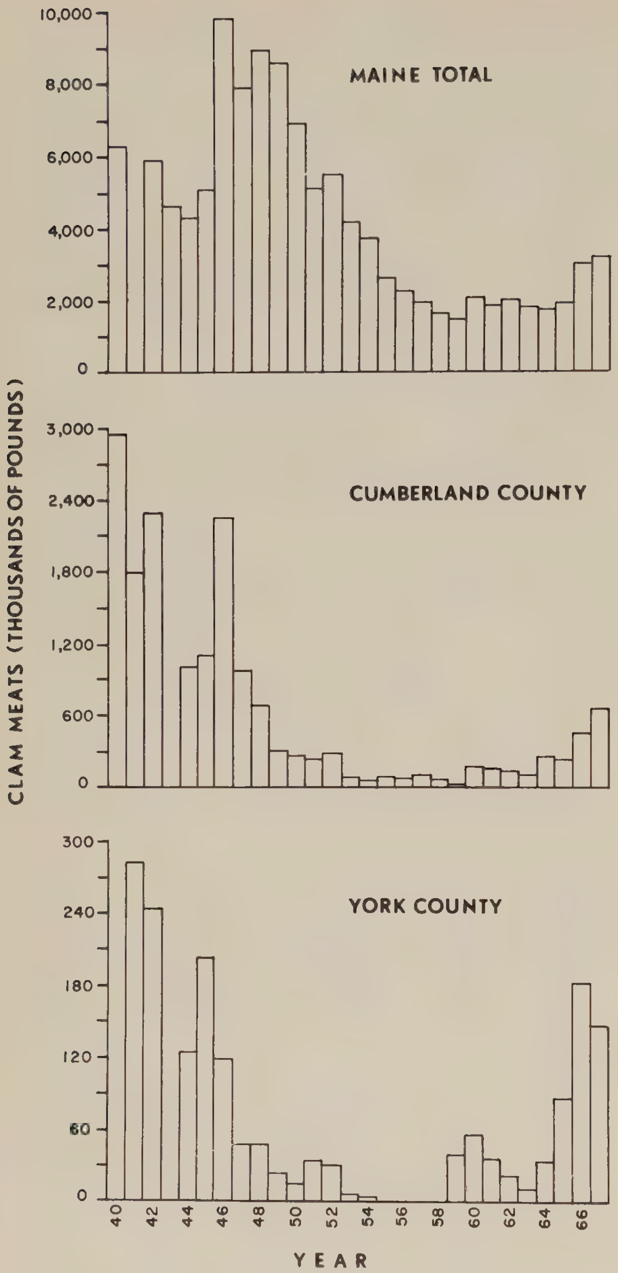

Figure 5.—Landings of soft-shell clams in Maine and Maine's southwestern counties, 1940–67. County totals for 1940–46 from Dow and Wallace (1961); Maine totals for 1940–56 from Power (1958); and county totals for 1947–67 and Maine totals for 1957–67 from Fish and Wildlife Service (1948–68). No totals were available for York County, 1940 and 1943; Cumberland County, 1943; and Maine, 1941. Landings in York County in 1955–58 were less than 300 lbs.

occur, however, until a certain stage of the warming trend had been reached.

Similarly, the effects of low temperature may be direct or indirect, short- or long-term. Broekhuysen's (1936) evidence and ideas on the deleterious effects of combined low temperature and low salinity may apply to upper estuaries and semienclosed bays. Since *Carcinus* consumes considerably more oxygen in dilute sea water than in water of normal salinity (Waterman, 1960), unfavorable temperature, salinity, and dissolved oxygen may combine to provide an environment lethal to *Carcinus*.

As the species ordinarily seems tolerant of low temperature, lowered salinity, or low dissolved oxygen when the conditions are met singly, it is more likely that widespread reduction in numbers results from more complex causes or chronic conditions. Examples might be the ones described in the foregoing section, "Relation of Crab Abundance to Temperature Change," in which unseasonable warming brought the normally dormant crabs out into the open where they were later killed by falling temperature, or where an excessively long dormant period, caused by a long, cold winter with heavy icing of the shore, may have been fatal.

In the northern part of its range, *Carcinus maenas* is apparently among the most responsive of common marine animals to temperature change; consequently, the species may be a useful indicator of changes in the environment that affect associated animals to a less obvious but perhaps no less serious extent.

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EGG-TO-MIGRANT SURVIVAL OF SPRING CHINOOK SALMON (*ONCORHYNCHUS TSHAWYTSCHA*) IN THE YAKIMA RIVER, WASHINGTON

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ABSTRACT

Egg-to-migrant survival for the 1957–61 broods ranged from 5.4 to 16.4 percent—the first estimates of survival of chinook salmon in a large river system.

Spring chinook salmon spawn in the American, Bumping, and Naches Rivers and Rattlesnake Creek—tributaries of the Yakima River—and in the upper stretch of Yakima River proper. For both sexes, spawning fish in the upper Yakima River are smaller than those in the other areas. Mean lengths (mideye to end of hypural plate) were 45.5 and 57.3 cm. for the males and females in the upper Yakima River and 65.4 and 71 cm. for the males and females in the other areas.

Spring chinook salmon migrate to sea in their second year. Larger fish migrate earlier in the season than do smaller fish. Seaward migration reaches a peak at Prosser, Wash., on the lower Yakima River between April 14 and May 19. Movement tends to be nocturnal.

Knowledge about the life history of a species of fish is fundamental to its effective management. For Pacific salmon (*Oncorhynchus* spp.), some conception is required of survival from the egg to the seaward migrant stage. Survival from egg to migrant has been measured for four of the five species that spawn in North America—sockeye, pink, chum, and coho salmon (*O. nerka*, *O. gorbuscha*, *O. keta*, and *O. kisutch*)—but comparable information is almost completely lacking for chinook salmon (*O. tshawytscha*). For the race of chinook salmon known as spring chinook, survival has never been measured mainly because this race spawns in large river systems where sampling is difficult.[1]

The Columbia River, although its runs have been reduced to a fraction of their former size, continues to be a major producer of spring chinook salmon. To estimate the egg-to-migrant survival of a population of spring chinook salmon, the Bureau of Commercial Fisheries began a study in 1957 on the Yakima River, a tributary of the Columbia River in south-central Washington (fig. 1). The Yakima River was chosen because a trap in a diversion canal at Prosser, Wash., on the lower river provided a unique opportunity to sample the seaward migration. The trap allowed us to estimate the number of seaward migrants each year. Comparison of the number of migrants with the number of eggs deposited by the female spawners in the appropriate brood year yielded an estimate of survival to the seaward migrant stage. This paper is a summary of our work on the Yakima River from 1957 to 1963.

SPAWNING OF SPRING CHINOOK SALMON

The aim of our studies of adult spring chinook salmon was to estimate the number of eggs deposited. We had to determine (1) the distribution and abundance of redds, (2) the size, age, and fecundity of the spawners, and (3) the number of eggs retained by female spawners.

DISTRIBUTION AND ABUNDANCE OF REDDS

The spawning grounds of spring chinook salmon in the Columbia River system were originally delineated in the 1930's (Bryant and Parkhurst, 1950). For the Yakima River system, the following

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[1] Seasonal races of chinook salmon in the Columbia River system are classified as spring, summer, or fall chinook depending on the time of year that the adults enter the river to spawn. In tributaries that contain more than one seasonal race, the spawning of spring chinook salmon is separated in time and space from the spawning of the other races.

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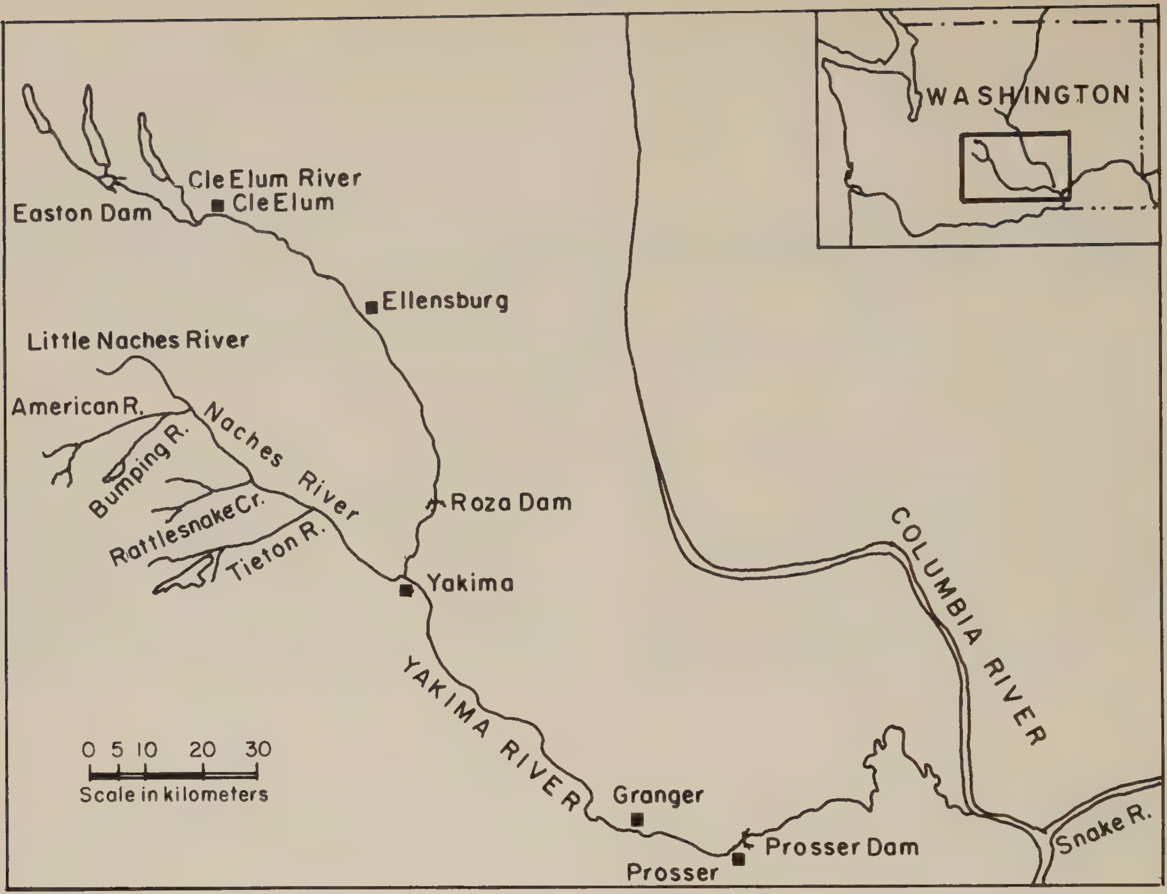
WASHINGTON
Cle Elum River
Easton Dam
Cle Elum
Ellensburg
Little Naches River
American R.
Naches River
Bumping R.
Rattlesnake Cr.
Tieton R.
Roza Dam
Yakima
COLUMBIA RIVER
YAKIMA RIVER
0 5 10 20 30
Scale in kilometers
Granger
Prosser Dam
Prosser
Snake R.

FIGURE 1.—Yakima River system and locations important to present study.

areas were listed: Yakima River from Easton Dam to Ellensburg, Naches River from the confluence of the Little Naches and Bumping Rivers to the confluence with the Tieton River, and Little Naches, Bumping, and American Rivers and Rattlesnake Creek. We surveyed these and other likely areas in 1957 but found that, except for a few scattered redds in the Cle Elum River, spawning was still confined to the areas reported by Bryant and Parkhurst (1950). We surveyed only the latter areas and the Cle Elum River in 1958–61.

Surveys were made in a standard manner. Working in pairs or alone, depending on the width of the stream, we counted the redds and the live fish as we waded downstream or floated downstream in rubber boats (table 1). If necessary, the surveys were repeated weekly until no unspawned fish were sighted. This precaution minimized the possibility that we might overlook redds made by females that were late arrivals.

Distribution of redds (fig. 2) varied little from year to year and agreed closely with Bryant and Parkhurst (1950).

TABLE 1.—*Number of spawning redds of spring chinook salmon in the Yakima River system, 1957–61*

Stream	Spawning redds				
	1957	1958	1959	1960	1961
Naches River and tributaries:	*Number*	*Number*	*Number*	*Number*	*Number*
American River	479	137	100	27	23
Bumping River	41	67	55	31	30
Little Naches River	106	16	22	3	2
Naches River	94	34	108	57	103
Rattlesnake Creek	44	30	21	8	8
Subtotal	764	284	306	126	166
Upper Yakima River: (Yakima River from Easton Dam to Ellensburg and the Cle Elum River)	1,216	531	255	184	175
Total	1,980	815	561	310	341

Spawning was distributed over a 6-week period. Peak of spawning was usually within the following dates:

American River, Aug. 8 to 12.
Bumping River, Sept. 5 to 10.
Little Naches River, Sept. 1 to 5.
Naches River, Sept. 1 to 5.
Rattlesnake Creek, Aug. 28 to Sept. 2.
Upper Yakima River, Sept. 17 to 22.

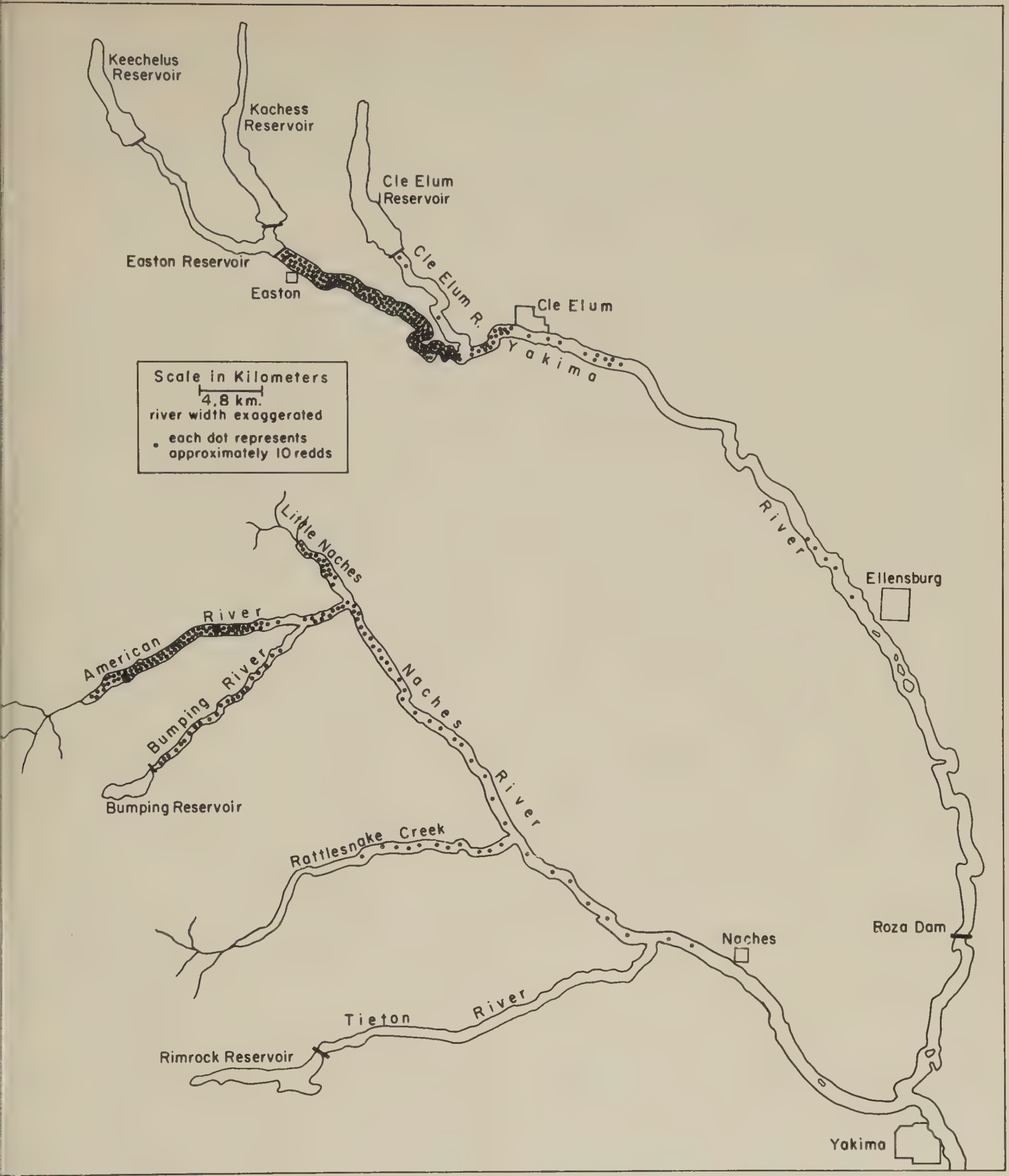
Keechelus Reservoir
Kachess Reservoir
Cle Elum Reservoir
Easton Reservoir
Easton
Cle Elum R.
Cle Elum
Yakima River
Scale in Kilometers
4.8 km.
river width exaggerated
each dot represents approximately 10 redds
Little Naches
American River
Bumping River
Bumping Reservoir
Naches River
Rattlesnake Creek
Ellensburg
Naches
Roza Dam
Tieton River
Rimrock Reservoir
Yakima

FIGURE 2.—Distribution of spawning redds of spring chinook salmon in the Yakima River system, 1957–61.

SIZE, AGE, AND FECUNDITY OF THE SPAWNERS

All of the spawned-out carcasses that could be retrieved were measured. Two measurements were obtained for each fish: fork length and mid-eye to posterior end of the hypural plate. The latter measurement excludes the snout and tail—appendages that are usually distorted on spawning salmon. The snout becomes elongated, particularly in the male, and the tail of the female is damaged in digging the redd.

Length-frequency curves by sex for the upper Yakima River and Naches River subareas (fig. 3) show that fish of both sexes are longer in the Naches River subarea than in the upper Yakima River subarea.[2] Mean lengths are 45.5 and 65.4 cm. for the males and 57.3 and 71 cm. for the females in the respective areas. The frequency distribution of length of males from the Naches River subarea is trimodal with peaks at 40, 61, and 79 cm. These modes correspond to those in samples of spring chinook salmon that are captured in the gill net fishery at the mouth of the Columbia River—fish that belong to age groups 1.1, 1.2, and 1.3, respectively.[3] Only two modes—at 40 and 55 cm.—appear in the length-frequency curve of males from the spawning area in the upper Yakima River subarea. These modes are comparable to the modes of the 1.1 and 1.2 age groups in the fishery. Females from the Naches River subarea have a single mode at 73 cm., which corresponds to the mode of females of the 1.3 age group in the fishery. Females from the upper Yakima River subarea have a single mode at 57 cm., which corresponds to the mode of the 1.2 age group in the fishery. We were unable to verify these gross length-age relations with scale data; the scales from spawned-out fish were so deteriorated that ocean ages were undeterminable.

NUMBER OF EGGS RETAINED BY FEMALE SPAWNERS

In 1960 and 1961, 82 females were examined for the number of eggs retained after spawning. Results were: 0 eggs—47 fish; 1 to 10 eggs—22 fish; 11 to 100 eggs—10 fish; and over 100 eggs—3 fish. The number of eggs retained by the spawning females does not appear to have any great effect on estimates of egg deposition.

ESTIMATED NUMBER OF EGGS DEPOSITED

Number of eggs deposited, $\hat{Y}$, was estimated by the formula

$$\hat{Y}=\sum_{i=1}^{6} n_i \hat{Y}_i$$

where n_i is the number of redds in stream (i), and $\hat{Y}_i$ is the estimated mean fecundity of the female spawners in stream (i). Here, in turn, $\hat{Y}_i = -3{,}634+105.51\ X_i$ where X_i is the mean fork length in cm. of female spawners in stream (i). The values −3,634 and 105.5 were reported by Galbreath and Ridenhour (1964), who investigated the fork length-fecundity relation of chinook salmon in the Columbia River. We used the dual measurements taken on the spawning grounds to convert to fork lengths the mideye to hypural plate measurements. These fork lengths are subject to error introduced by the elongation of the snout in the male and the wearing away of the caudal fin rays of the female in redd building. Although we were unable to measure this error, we believe it to be small.

The number of eggs deposited in the Yakima River system as a whole and that of each subarea declined markedly between 1957 and 1961 (table 2).

SEAWARD MIGRATION AND SURVIVAL OF PROGENY

We designed our studies with young salmon to estimate the number of fish that migrated seaward each spring. To make this estimate, we trapped and counted a sample of migrating fish each day during the 1959–63 migrations and from these partial counts made daily and seasonal estimates.

Sampling was at Prosser, Wash., on the lower Yakima River where a 3-m.-high dam creates a pool from which a canal transports water to a power plant 25 km. downstream. A battery of electrically powered rotary screens, 1.6 km. downstream from the entrance of the canal, diverts fish into an underground conduit which returns fish to the river. Just before it reenters the river, the conduit is equipped with a trapping system which, when activated, captures all fish that are being returned to the river (fig. 4). An aerial photograph of the area was the basis for a

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[2] The upper Yakima River subarea, by our definition, includes that part of the Yakima River and its tributaries that lies above the confluence of the Yakima and Naches Rivers; the Naches River subarea includes the Naches River and its tributaries; and the main Yakima River is that part of the river that lies downstream from the confluence of the Naches and Yakima Rivers.

[3] The method of designating age follows the scale formulas of Koo (1962). The number of winters at sea is shown by an Arabic numeral preceded by a dot; similarly, the number of winters that the salmon spent in fresh water (not counting the winter the egg was in gravel) is shown by an Arabic numeral preceding a dot. Both are shown by two Arabic numerals separated by a dot. A salmon of age 1.2 spent 1 winter in fresh water and 2 winters in the ocean; the fish is 3 years old and in its fourth year of life.

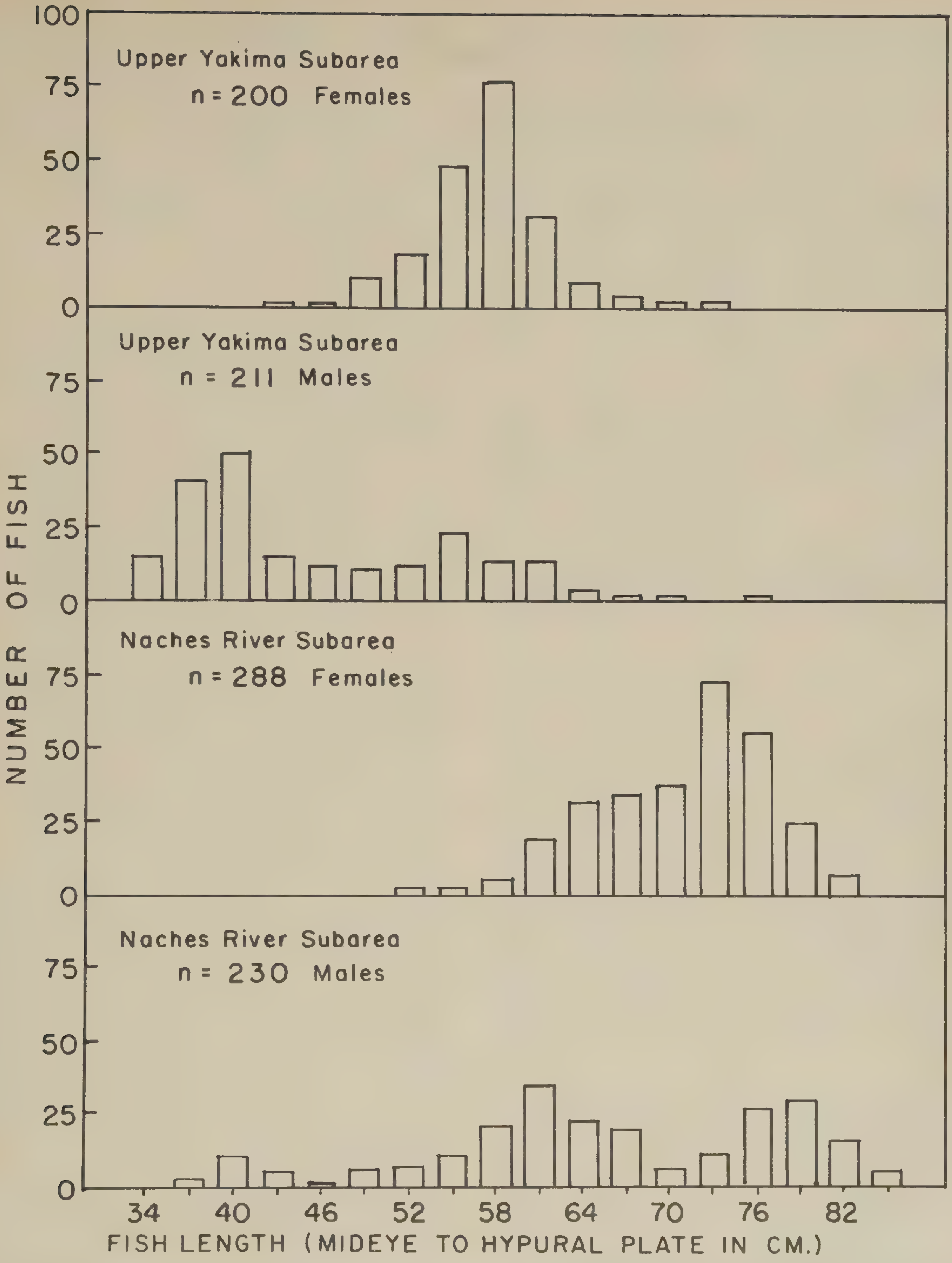

FIGURE 3.—Length-frequency distribution of adult spring chinook salmon in the Yakima River system, 1957–61.

TABLE 2.—*Estimates of number of eggs deposited by spring chinook salmon in the Yakima River system, 1957–61*

Year, subarea, and stream	Redds counted	Mean fork length of female spawner	Mean fecundity	Eggs deposited
1957:	*Number*	*Centimeters*	*Number of eggs*	*Millions*
Naches subarea:				
American River	479	86 1.	5,446	2.609
Bumping River	41	87.1	5,553	.228
Little Naches River	106	80.7	4,877	.517
Naches River	94	85.2	5,354	.503
Rattlesnake Creek	44	80.2	4,832	.213
Subtotal	764			4.070
Upper Yakima subarea	1,216	70.3	3,784	4.600
Total	1,980			8.670
1958:				
Naches subarea:				
American River	137	86.1	5,448	.747
Bumping River	67	80.8	4,888	.328
Little Naches River	16	84.0	5,231	.084
Naches River	34	84.3	5,255	.179
Rattlesnake Creek	30	81.1	4,926	.148
Subtotal	284			1.486
Upper Yakima subarea	531	66.1	3,342	1.774
Total	815			3.260
1959:				
Naches subarea:				
American River	100	89.7	5,831	.583
Bumping River	55	81.5	4,961	.273
Little Naches River	22	84.7	5,304	.117
Naches River	108	86.0	5,443	.588
Rattlesnake Creek	21	78.4	4,639	.097
Subtotal	306			1.658
Upper Yakima subarea	255	68.2	3,565	.910
Total	561			2.568
1960:				
Naches subarea:				
American River	27	84.2	5,250	.142
Bumping River	31	81.7	5,003	.155
Little Naches River	3	82.6	5,081	.015
Naches River	57	79.5	4,754	.271
Rattlesnake Creek	8	80.2	4,832	.039
Subtotal	126			.622
Upper Yakima subarea	184	66.3	3,358	.618
Total	310			1.240
1961:				
Naches subarea:				
American River	23	86.2	5,459	.126
Bumping River	30	80.1	4,816	.144
Little Naches River	2	82.6	5,081	.010
Naches River	103	86.2	5,464	.563
Rattlesnake Creek	8	80.6	4,867	.039
Subtotal	166			.882
Upper Yakima subarea	175	68.2	3,564	.624
Total	341			1.506

sketch to describe the function of the canal-conduit system. The trapping system is shown diagrammatically in figure 5.

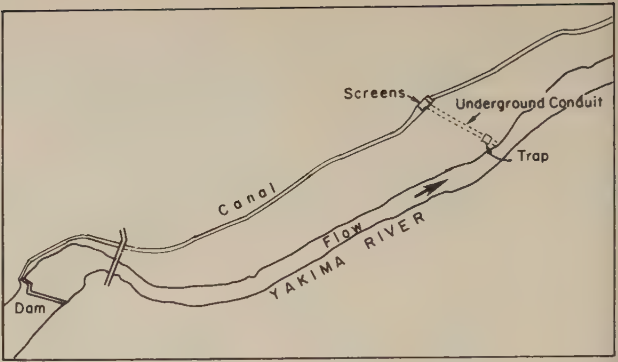

FIGURE 4.—Diagrammatic sketch of the system for sampling the seaward migration at Prosser. Low dam diverts water into the canal; screens divert fish into an underground conduit that carries them to the traps and eventually to the river.

Procedures for studying seaward migration were similar for all years. Trapping began about April 1 when young salmon were not yet abundant and continued until they became scarce—sometime in June. Fish were removed from the trap with dip nets at 8 a.m., 12 noon, 4 p.m., and 12 midnight. The trapping "day" used here extended from 8 a.m. of the calendar day indicated to 8 a.m. of the following day. Fish other than salmon were counted and released. Young salmon were transferred into tubs for closer inspection before they were counted and released.

Once a week a sample of young chinook salmon was anesthetized in a 1:20,000 solution of MS 222. Fork length to the nearest millimeter was recorded from each fish. Weight to the nearest gram was recorded from a randomly selected subsample of about 50 fish per week. Scales, selected from a stratified subsample, were placed between pairs of glass slides and later examined with a microscope to determine the age of the fish.

AGE AND SIZE OF SEAWARD MIGRANTS

Scales from 1,458 young chinook salmon captured at Prosser from 1959–63 revealed that fish were either in their first or second year of life. Certain differences between the age groups are noteworthy. First, the two age groups do not appear at Prosser at the same time; fish that are in their second year appear in early April, but fish that are in their first year do not appear until June. Second, when samples that contain fish of both age groups are viewed in tubs, the first-year fish (even the few that are as long as the fish in their second year) are readily distinguishable by their stouter bodies.

We reasoned that the stouter, first-year migrants were not spring chinook salmon but rather fall chinook salmon—progeny of adult fall chinook salmon that spawn near Granger, 40 km. upstream from Prosser. If they were spring chinook salmon migrating downstream from the upriver spawning areas, they would have had to move through the midriver areas in the winter or spring. But this movement did not take place. We sampled the Yakima River system extensively with electro-

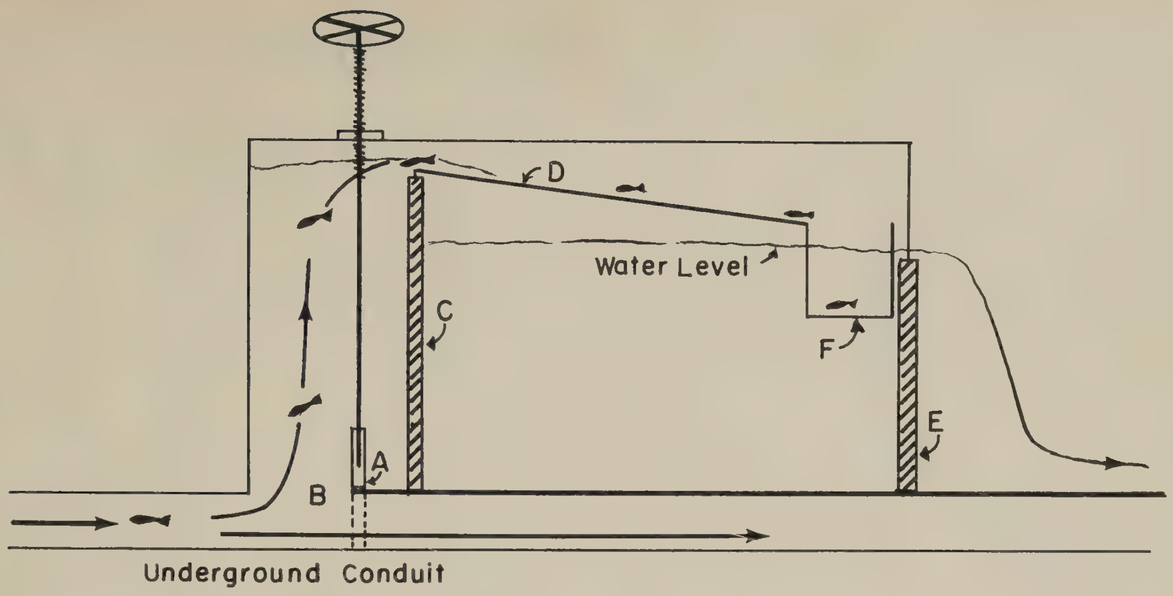

FIGURE 5.—Diagrammatic sketch of trapping system on bypass conduit on the Yakima River at Prosser. When valve (A) is open, fish pass directly to the Yakima River. To activate the trap, the valve is closed forcing the water and fish upward through a hole in the top of the conduit (B). Water flows over the top of the interior wall (C), through inclined plane screen (D), over a second interior wall (E), and on to the Yakima River. Fish and some water continue into trap (F).

fishing equipment in the winter and spring of 1958–63 but found no first-year fish in the mid-river stretches. Furthermore, no first-year fish migrated seaward past Roza Dam, 19 km. above the confluence of the Yakima and Naches Rivers, in either 1961 or 1962 (according to Donald Greenland).[4] Data presented here pertain only to spring chinook salmon, or fish that migrate seaward in their second year.

Length-frequency polygons of downstream-migrating spring chinook salmon (fig. 6) show that the modal length increased from 120 mm. in 1959 and 1960 to 125 mm. in 1961, 130 mm. in 1962, and 135 mm. in 1963. Present data are inadequate to explain the reason for the increase in modal length. Possible explanations include the availability of more food per young fish and differential growth and abundance of the several tributary subpopulations believed to be present.

Analysis of the length and weight data (table 3 and figure 7) clearly shows that the larger fish tend to migrate early in the season. The condition factor tends to increase—that is, the fish become heavier per unit length as the season progresses. This change is explained, at least in part, by the extended sojourn of the later migrating fish in water where the temperature is rising and food is becoming more abundant, and where their feeding becomes more intensive.

TIMING OF SEAWARD MIGRATION

The daily timing of the downstream migrations in 1959–63 was similar for all years (fig. 8). Generally the catches remained relatively stable between periods ending at noon, 4 p.m., and 8 p.m. and increased in the period ending at midnight. The hourly distribution of the catch between midnight and 8 a.m. is unknown, but the number of chinook salmon captured during the 8-hour period approximated the number taken from 8 p.m. to midnight. Thus, migration tended to be at night.

The week or weeks of heaviest seaward migration of spring chinook salmon at Prosser varied in 1959–63, but always fell between April 14 and May 19 (fig. 9).

SURVIVAL TO SEAWARD MIGRATION

We estimated the number of seaward migrants from the formula:

$$\hat{N}=\sum_{i=1}^{n}\hat{N}_i=\sum_{i=1}^{n}Ci(32.5/f_i)$$

where $\hat{N}$ is the estimated number of spring chinook salmon migrating seaward, $\hat{N}_i$ is the estimated

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[4] Donald Greenland, Fishery Biologist, Bur. Commer. Fish., Columbia River Program Office, Portland, Oreg. Personal communication.

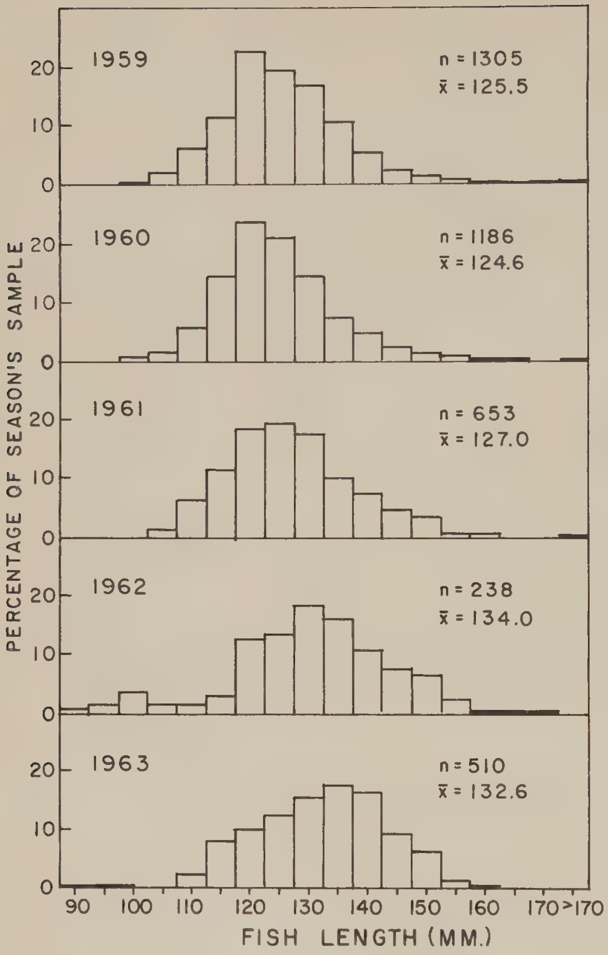

FIGURE 6.—Length-frequency distribution of Yakima River spring chinook salmon captured during their seaward migration at Prosser, 1959–63.

TABLE 3.—*Mean length, mean weight, condition factor, and size of samples of spring chinook salmon taken at Prosser, 1959–63*

Date (week ending)	Fish	Mean fork length	Mean weight	Condition factor
	Number	*Millimeters*	*Grams*	
1959:				
April 14	50	128.4	23.8	1.13
21	50	129.6	24.4	1.12
28	49	127.7	23.2	1.12
May 5	50	121.8	20.7	1.15
12	50	122.9	20.1	1.08
19	48	120.0	20.0	1.16
26	50	124.0	21.9	1.15
June 2	29	125.3	22.8	1.16
9	15	119.5	20.0	1.17
After June 9	23	117.6	19.5	1.20
1960:				
April 7	28	130.5	24.1	1.09
14	50	125.3	20.7	1.06
21	50	132.7	25.3	1.08
28	53	127.7	21.9	1.05
May 5	102	123.8	20.0	1.06
12	50	125.8	21.8	1.10
19	49	119.2	19.1	1.13
26	50	123.8	20.7	1.09
June 2	50	121.4	20.3	1.13
9	50	120.4	20.7	1.19
After June 9	51	121.8	21.8	1.21
1961:				
April 7	52	132.3	25.2	1.09
14	50	136.0	26.9	1.07
21	50	124.7	21.0	1.08
28	50	130.2	23.2	1.05
May 12	104	123.6	20.8	1.10
19	48	120.4	19.2	1.10
June 9	19	118.3	18.7	1.13
1962:				
April 14	50	137.7	28.7	1.10
21	50	139.4	29.6	1.09
28	50	130.3	23.7	1.07
May 19	33	125.7	21.7	1.09
June 2	37	129.5	24.5	1.13
After June 9	18	127.9	25.0	1.19
1963:				
April 7	30	143.9	31.6	1.06
14	33	138.2	29.6	1.12
21	38	141.4	29.7	1.05
28	45	138.6	28.4	1.07
May 5	110	133.5	26.7	1.12
12	40	136.3	27.3	1.08
19	37	131.8	24.2	1.06
26	42	130.7	23.8	1.07
June 2	32	127.8	21.7	1.04
9	60	120.1	19.0	1.10
After June 9	42	121.4	20.7	1.16

TABLE 4.—*Egg-to-migrant survival of young spring chinook salmon in the Yakima River (brood years 1957–61)*

Brood year	Egg deposited	Seaward migration	Survival
	Millions	*Thousands*	*Percent*
1957	8.670	464	5.4
1958	3.260	319	9.8
1959	2.568	194	7.6
1960	1.240	177	14.3
1961	1.505	246	16.4

number migrating on day (i), Ci is the number captured in the trap on day (i), and f_i is the estimated flow in cubic meters per second of the Yakima River at Prosser on day (i) (U.S. Geological Survey, 1961–65). Canal flow is constant at 32.5 m.^{3} per second. This method requires the assumptions that the number of fish per volume of water is the same in the canal as in the river and that the mortality in the canal is the same as that in the adjacent stretch of river. The number of migrants that were caught in the trap and the total number that we estimated to have migrated seaward at Prosser are shown in figure 10 by day and year.

Estimates of the number of seaward migrants, estimates of the number of eggs deposited in the appropriate brood year, and the percentage survival are shown in table 4 and figure 11. Survival ranged from 5.4 to 16.4 percent; the average was 10.7 percent. The low survival of the 1957 brood was caused—to a great extent—by an unnatural condition that did not recur in the other years. In 1957 an estimated 30 to 50 percent of the eggs deposited in the upper Yakima River subarea succumbed to exposure when, in October and November, the water level was artificially lowered and maintained 2 feet below what it had

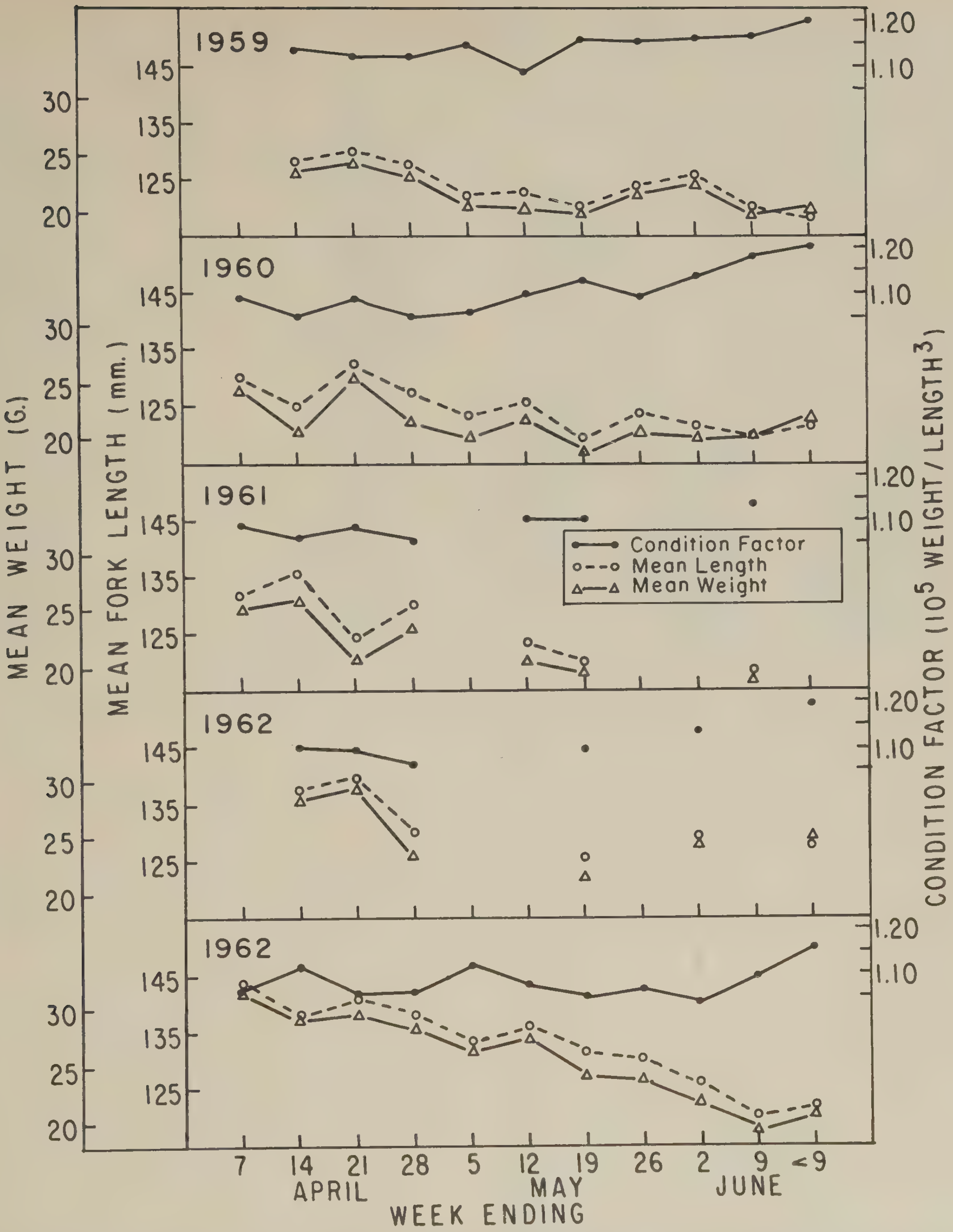

FIGURE 7.—Mean length, mean weight, and condition factor of Yakima River spring chinook salmon captured during their seaward migration at Prosser, 1959–63.

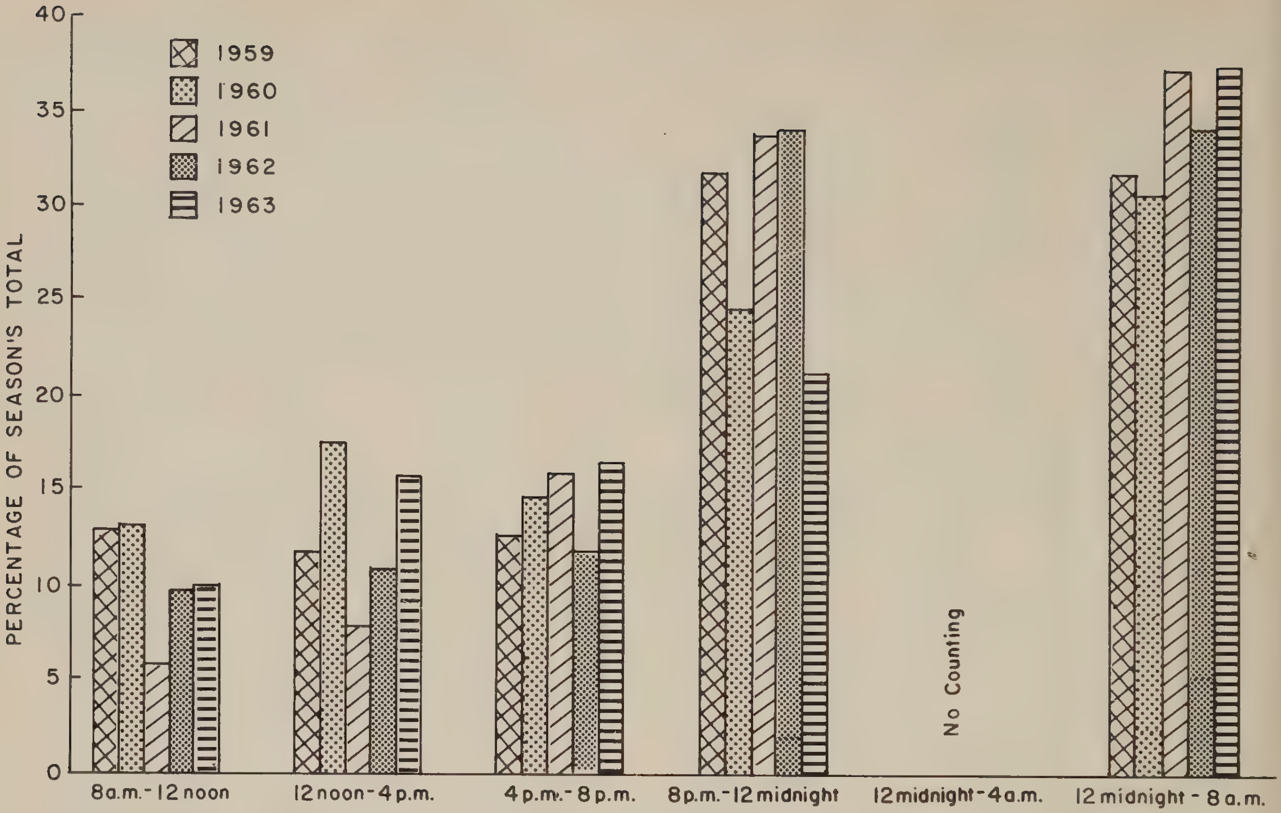

FIGURE 8.—Daily distribution of Yakima River spring chinook salmon captured during their seaward migration at Prosser, 1959–63.

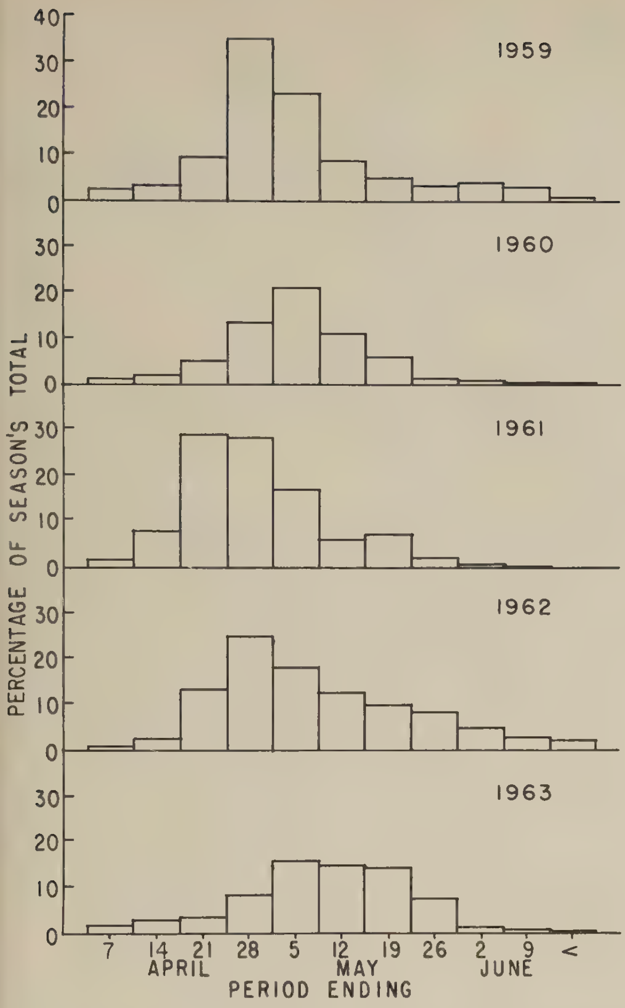

FIGURE 9.—Seasonal distribution of Yakima River spring chinook salmon captured during their seaward migration at Prosser, 1959–63.

been when the fish spawned in late September (Quentin Edson).[5] In subsequent years, per an agreement between the State of Washington Department of Fisheries and the U.S. Bureau of Reclamation—the agency controlling the flow of water over Easton Dam, a relatively uniform minimum flow was maintained from September until February when the young fish emerge from the gravel.

TABLE 5.—*Survival from egg to seaward migrant for five species of Pacific salmon*

Species and location	Survival, egg to seaward migrant		Period	Source of information
	Range	Average		
	Percent	*Percent*	*Years*	
Sockeye salmon:				
Cultus Lake, B.C	1.01– 3.22	1.87	4	Ricker, 1966.
Babine Lake, B.C	1.34– 5.18	3.77	5	Do.
Lakelse Lake, B.C	.60– 5.05	1.86	7	Do.
Port John Lake, B.C		3.00	(1)	Do.
Chilko Lake, B.C		8.00	(1)	Do.
Dalnee Lake, U.S.S.R	.005– 1.05	.28	10	Hanamura, 1966.
Pink salmon:				
McClinton Creek, B.C	6.90–23.80	(1)	6	Neave, 1966a.
Morrison Creek, B.C	4.70– 6.70	(1)	2	Do.
Hooknose Creek, B.C	.90–37.20	(1)	13	Do.
Lakelse River, B.C	18.00	(1)	1	Do.
Kispiox River, B.C	23.00	(1)	1	Do.
Kitwanga River, B.C	15.00	(1)	1	Do.
Wahleach Creek, B.C	37.00	(1)	1	Do.
Sashin Creek, Alaska	.10–21.80	6.33	22	McNeil, 1966.
Karymai Spring, U.S.S.R.	.02– 5.70	1.96	6	Semko, 1954.
Chum salmon:				
Nile Creek, B.C	.08–13.60	(1)	8	Neave, 1966b.
Hooknose Creek, B.C	.96–22.00	0	13	Do.
Karymai Spring, U.S.S.R.	.68– 4.20	2.16	7	Semko, 1954.
Coho salmon:				
Nile Creek, B.C	.76– 2.10	1.27	4	Godfrey, 1965.
Hooknose Creek, B.C	.70– 3.96	1.30	10	Do.
Minter Creek, Wash	.70– 9.65	1.71	11	Do.
Waddel Creek, Calif	1.16– 1.56	1.43	4	Do.
Chinook salmon:				
Fall Creek, Calif	7.00–32.00	14.50	4	Wales and Coots, 1955.
Yakima River, Wash	5.35–16.35	10.70	5	Present study.

[1] Not reported.

Estimates of survival from the egg to the seaward migrant stage for Pacific salmon are summarized in table 5. Prior to the present study, survival of chinook salmon had been estimated only in Fall Creek, Calif., and the usefulness of these values is limited. Fall Creek is a small atypical spawning stream and the progeny of the Fall Creek chinook salmon population migrate to sea in their first year of life (a characteristic of fall chinook, pink, and chum salmon, but not of spring or summer chinook salmon; the latter races, like sockeye and coho salmon, usually spend 1 year or more in fresh water before migrating to sea).

Relative to all other species, the limits within which the percentage survival of spring chinook salmon in the Yakima River fluctuates are neither wide nor narrow but reasonably moderate. Egg-to-migrant survival of spring chinook salmon in the Yakima River is generally higher than that for sockeye salmon and coho salmon—other species whose young spend 1 year or more in fresh water. The results of the various studies are not strictly comparable, however, because migrants are trapped at varying and sometimes unspecified points in time and distance from the nursery areas and the sea. Young spring chinook salmon trapped at Prosser must yet migrate 600 km. to the sea.

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[5] Quentin Edson, Fishery Biologist, City of Tacoma, Department of Public Utilities, Tacoma, Washington. Personal communication.

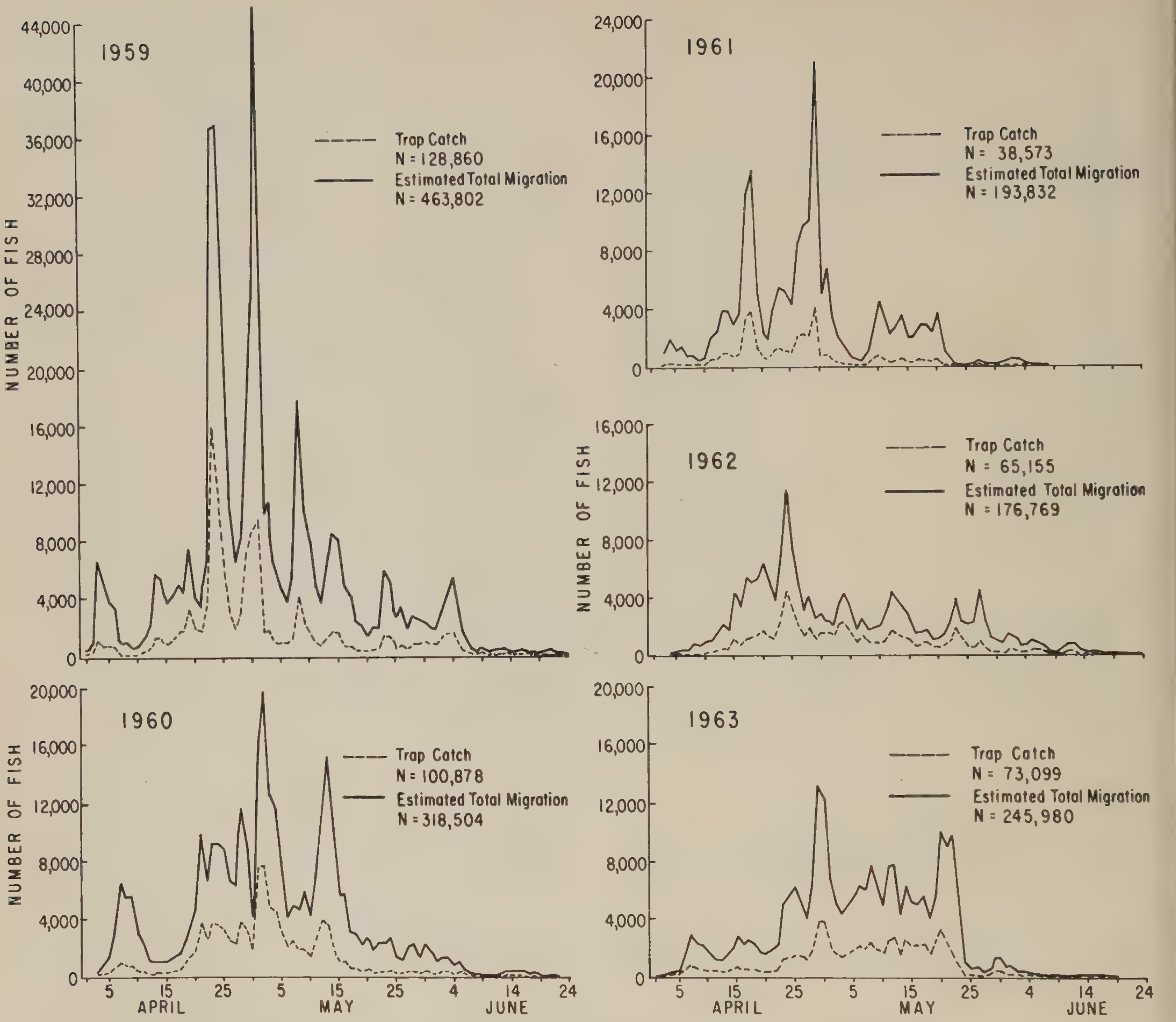

Figure 10.—Seaward migration of Yakima River spring chinook salmon at Prosser, 1959–63. Number captured in the trap are shown by broken lines. Solid lines indicate the calculated totals for the entire river (trap and remainder of the river).

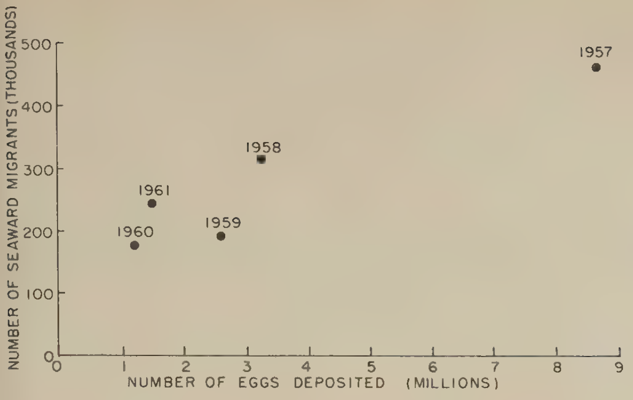

FIGURE 11.—Estimated number of seaward migrants and estimated number of eggs deposited, Yakima River spring chinook salmon, brood years 1957–61.

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CONTRIBUTION OF COLUMBIA RIVER HATCHERIES TO HARVEST OF FALL CHINOOK SALMON (*Oncorhynchus tshawytscha*)

BY DONALD D. WORLUND,[1] ROY J. WAHLE,[2] AND PAUL D. ZIMMER[2]

ABSTRACT

A marking experiment was designed in which fall chinook salmon (*Oncorhynchus tshawytscha*) from 12 Columbia River hatcheries were marked in 4 consecutive years to estimate their contribution to the sport and commercial fisheries. The study was planned and is being executed by scientists of the Fisheries Research Board of Canada, Bureau of Commercial Fisheries, and fishery agencies of the States of Washington, Oregon, California, and Alaska.

Sampling for marked fish is being conducted in most ocean fisheries for chinook salmon from Monterey, Calif., to southeast Alaska, as well as on the Columbia River. The 1963–66 returns from the first year's release (1961 brood) of 5.4 million marked fish make it possible to obtain a preliminary estimate of the contribution of the total hatchery releases as represented by this marked group.

The estimated catch of 1961-brood fish that originated from the hatcheries under study was 287,326, or about 10 percent of the total catch of chinook salmon of that brood in the fisheries sampled. The estimated net value of this catch (to the fisherman) was about $1,900,000, whereas the cost to produce them was $831,000. The benefit to cost ratio was 2.3:1.

The net value of the catch of fall chinook salmon of the 1961 brood that originated from all Columbia River hatcheries (including those not participating in the marking experiments) was estimated at $2,055,000.

The U.S. Fish and Wildlife Service has financed the Columbia River Fishery Development Program, a cooperative effort of the States of Oregon, Washington, and Idaho, since its inception in 1949. The Bureau of Commercial Fisheries Columbia Fisheries Program Office, Portland, Oreg., administers this project, which is designed to increase production of salmon (*Oncorhynchus* spp.) and steelhead trout (*Salmo gairdneri*) in the Columbia River.

A major accomplishment of the program has been the construction and modernization of 19 salmon producing hatcheries on the lower 290 km. (180 miles) of the river. These hatcheries, managed by the Bureau of Sport Fisheries and Wildlife and the States of Washington and Oregon, were built primarily to offset the loss of natural spawning and rearing areas for salmon and steelhead trout caused by water development projects.

Releases of fall chinook salmon have varied from less than 10 million fish from 6 hatcheries in 1949 to about 56 million from 14 hatcheries in 1966. The contribution of these large releases to the commercial and sport fisheries, however, is unknown. Past marking experiments have demonstrated that hatchery releases contribute to the fisheries, but because such experiments were limited and designed for other purposes, the contribution has not been estimated.

A marking experiment was undertaken in 1962 by the Columbia Fisheries Program Office to estimate the contribution of hatchery-reared fall chinook salmon to the fisheries. The experiment was confined to 12 hatcheries that have propagated about 90 percent of all fall chinook salmon artificially reared in the Columbia River. Data collection will be completed by the end of 1969; however, sufficient information is presently available for preliminary estimates of the contribution to the fisheries by one group (1961 brood) of hatchery-reared fall chinook salmon.

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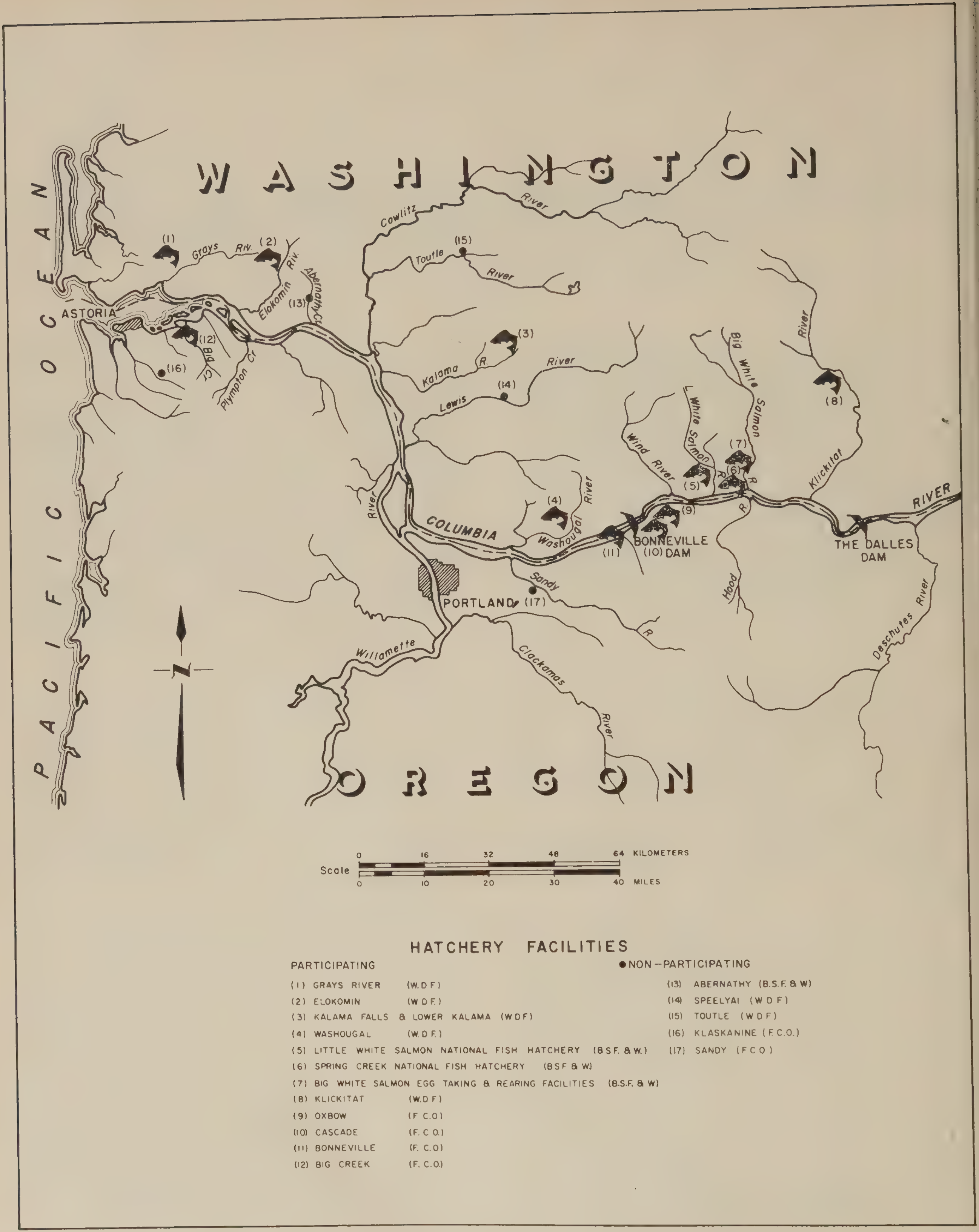
WASHINGTON
OREGON
PACIFIC OCEAN
ASTORIA
PORTLAND
COLUMBIA RIVER
BONNEVILLE DAM
THE DALLES DAM
Grays Riv.
Elokomin Riv.
Abernathy Cr.
Big Cr.
Plympton Cr.
Cowlitz River
Toutle River
Kalama R.
Lewis River
Washougal River
Wind River
L. White Salmon R.
Big White Salmon R.
Klickitat River
Hood R.
Deschutes River
Sandy R.
Willamette River
Clackamas River
N
Scale
0 16 32 48 64 KILOMETERS
0 10 20 30 40 MILES
HATCHERY FACILITIES
PARTICIPATING
(1) GRAYS RIVER (W.D.F.)
(2) ELOKOMIN (W.D.F.)
(3) KALAMA FALLS & LOWER KALAMA (W.D.F.)
(4) WASHOUGAL (W.D.F.)
(5) LITTLE WHITE SALMON NATIONAL FISH HATCHERY (B.S.F. & W.)
(6) SPRING CREEK NATIONAL FISH HATCHERY (B.S.F. & W.)
(7) BIG WHITE SALMON EGG TAKING & REARING FACILITIES (B.S.F. & W.)
(8) KLICKITAT (W.D.F.)
(9) OXBOW (F.C.O.)
(10) CASCADE (F.C.O.)
(11) BONNEVILLE (F.C.O.)
(12) BIG CREEK (F.C.O.)
● NON-PARTICIPATING
(13) ABERNATHY (B.S.F. & W.)
(14) SPEELYAI (W.D.F.)
(15) TOUTLE (W.D.F.)
(16) KLASKANINE (F.C.O.)
(17) SANDY (F.C.O.)

FIGURE 1.—Locations of fall chinook salmon hatcheries on lower Columbia River.

The 12 hatcheries are distributed over about 250 km. (155 miles) of the Columbia River (fig. 1). Big Creek Hatchery, the lowermost station, and Klickitat Hatchery, the uppermost, are on tributaries about 40 and 290 km. (25 and 180 miles), respectively, above the river mouth. Some hatcheries (Bonneville, Cascade, Oxbow, Little White Salmon, and Spring Creek) are adjacent to the Columbia River and release their fish directly into the river. In contrast, fish released at Klickitat Hatchery must travel about 40 km. (25 miles) to reach the main stem of the Columbia.

Artificial propagation procedures are similar at all hatcheries raising fall chinook salmon. Adults normally return to these hatcheries and are spawned during September and October. Depending upon water temperatures, fry typically reach the free swimming stage in February or March and are then placed in ponds. The young fish are released from the hatchery 90 to 120 days later at an average length of 6 to 8 cm. (2–3 inches). During the following 5 years, they are available to commercial and sport fisheries from southeast Alaska to central California. Some fish mature and return to the Columbia River during their second, third, fourth, and fifth years; however, most are in their third (age 3) and fourth years.

This report (1) describes the design of the marking experiment and (2) presents an estimate of the contribution (catch) to the fisheries by the 1961-brood hatchery releases and an estimate of the benefit-cost ratio. This is the first basic analysis of data collected under the hatchery evaluation study directed by Paul D. Zimmer of the Columbia River Fishery Development Program. Several research laboratories and individuals are analyzing data from this study and will develop much additional information.

DESIGN OF EXPERIMENT TO ESTIMATE HATCHERY CONTRIBUTION TO FISHERIES

The general approach for estimating the hatchery contribution of fall chinook salmon was to identically mark the same fraction (about 10 percent) of each hatchery's production and then sample for this mark in the commercial and sport fisheries. From the number of marked fish recovered and the sampling ratio, together with the fraction originally marked (or expected marked to unmarked ratio), we can estimate the number of hatchery–reared fall chinook salmon in the catch. In addition to the "common mark" (i.e., mark applied to portion of fish at all hatcheries under study), "special marks" were used at selected hatcheries each year to examine the variations in contribution among hatcheries. Supplemental data were also collected in an attempt to explain the expected variations among hatcheries and to test some of the assumptions underlying the experimental techniques and estimating procedures.

The success of the marking experiment required the efforts of many people and the cooperation of fishery agencies on the Pacific Coast (table 1). All marking and mark recovery activities were under the direct supervision of experienced biologists.

MARKING

The marking phase of the study began in June 1962 and was completed in June 1965. The 1961–64 broods (progeny of adults that spawned in 1961, 1962, 1963, and 1964) were marked. The "common mark" consisted of removing the adipose fin and a portion of the right or left maxillary bone. The clipped right maxillary was used to identify the 1961 and 1963 broods and the clipped left maxillary the 1962 and 1964 broods (table 2).

TABLE 1.—*Responsibilities of agencies participating in the marking and mark recovery phases of the Columbia River fall chinook hatchery contribution study, 1962–68*

Function	Execution	Supervision	Agency [1]
Coordinating and supervising	Biologist	Biologist	BCF
Obtaining fish for marking	Hatchery personnel	Biologist and hatchery manager	WDF, FCO, BSFW
Marking	Fish markers	Biologist	WDF, FCO, BSFW
Sampling hatchery releases.	Hatchery personnel	Biologist and hatchery manager	WDF, FCO, BSFW
Sampling catch for marked fish	Mark samplers	Biologist	ADFG, FRBC, WDF, FCO OGC, CFG, BCF
Sampling hatchery returns and natural spawning populations for marked fish.	do	do	WDF, FCO, BSFW

[1] ADFG—Alaska Dept. of Fish and Game; FRBC—Fisheries Research Board of Canada; WDF—Washington Dept. of Fisheries; FCO—Fish Commission of Oregon; OGC—Oregon Game Commission; CDFG—California Dept. of Fish and Game; BCF—Bureau of Commercial Fisheries; BSFW—Bureau of Sport Fisheries and Wildlife.

TABLE 2.—*Ages of marked Columbia River fall chinook salmon in catches and escapements by brood (1961–64) and sampling years (1963–69)*

Brood	Mark[1]	Release site	Year of sampling						
			1963	1964	1965	1966	1967	1968	1969
			Years old						
1961	Ad-RM	12 hatcheries	2	3	4	5			
	Ad-LV-RM	Spring Creek	2	3	4	5			
	Ad-RV-RM	Kalama	2	3	4	5			
	RV-RM	Ox Bow	2	3	4	5			
	LV-RM	Elokomin	2	3	4	5			
1962	Ad-LM	12 hatcheries		2	3	4	5		
	Ad-LV-LM	Spring Creek		2	3	4	5		
	Ad-RV-LM	Kalama		2	3	4	5		
	RV-LM	Cascade		2	3	4	5		
	LV-LM	Grays River		2	3	4	5		
1963	Ad-RM	12 hatcheries			2	3	4	5	
	Ad-LV-RM	Spring Creek			2	3	4	5	
	Ad-RV-RM	Kalama			2	3	4	5	
	RV-RM	Klickitat			2	3	4	5	
	LV-RM	Big Creek			2	3	4	5	
1964	Ad-LM	12 hatcheries				2	3	4	5
	Ad-LV-LM	Spring Creek				2	3	4	5
	Ad-RV-LM	Kalama				2	3	4	5
	RV-LM	Little White Salmon.				2	3	4	5
	LV-LM	Bonneville				2	3	4	5
Number of marks in catches and escapements			5	10	15	20	15	10	5

[1] Ad: Adipose; LV: Left ventral; RV: Right ventral; LM: Left maxillary; RM: Right maxillary.

To obtain the fish for marking, a sampling tool (Hewitt and Burrows, 1948) was modified to remove a random "10 percent" sample. This device is a circular net consisting of 10 equal pie-shaped sections that fits into a cylindrical liner such that all fish contained in the cylinder must pass through one of the sections (fig. 2). The sample for marking was obtained by closing one of the sections. In practice, the sampling device was placed in a tub partially filled with water. Fish were removed from a pond in groups weighing about 18 kg. (40 pounds) each and placed in the sampler, and the device was then raised; the closed section retained the sample for marking. The fish that passed through the open sections remained in the tub and were placed in another pond. This procedure was followed until all fish in each pond were processed.

At each hatchery, fish selected for marking were first anaesthetized with MS–222 [3] (tricaine methanesulfonate), then the markers used bent-nosed dissecting scissors to remove certain fins and maxillaries. Marked fish were held in hatchery troughs for recovery from the anaesthetic and returned to the group of unmarked fish from which they were removed. To ensure proper control of quality, 25 marked fish from each marker were examined daily. In addition, fish that died shortly after marking were carefully examined in an effort to detect improper handling.

The entire production of each hatchery was sampled at time of release (3–8 weeks after marking) to estimate the proportion and numbers of marked fish released. The procedure for obtaining this sample was the same as for selecting fish for marking, except that fish initially removed by the closed section of the sampler were pooled and sampled again. The resultant sample (about 1 percent of the total production) was sorted into marked and unmarked groups and counted and weighed. These counts, together with an estimate of the proportion removed by the particular sampler, were used to estimate the proportions and numbers of marked fish in the release.

RECOVERY OF MARKS

The recovery phase of the investigation began in 1963 and will end in 1969 (table 2).

Sampling for marked fish was designed to cover four areas: major ocean fisheries from southeast Alaska to central California, Columbia River fisheries, parent hatcheries, and certain natural spawning grounds.

Sampling for marks in each area consists of recording numbers of fish examined for marks and the numbers recovered with each type of mark. In addition, all marked fish and a sample of unmarked fish are examined for age, length, and weight. It was recognized that occurrence of marks and compositions of age and size would change with time; thus, the sampling season was stratified into small units (usually biweekly for the ocean and weekly for the Columbia River fisheries).

The general fisheries being sampled are ocean commercial and sport; Columbia River commercial and sport; and Puget Sound sport. For purposes of sampling, most fisheries were further stratified by port of landing. Exceptions are the Alaska and British Columbia troll, purse seine, and gill net fisheries; Columbia River commercial and sport fisheries; and Puget Sound sport fishery, in which the stratification is by area of catch. The specific fisheries being sampled are listed in table

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[3] Trade names referred to in this publication do not imply endorsement of commercial products by the Bureau of Commercial Fisheries.

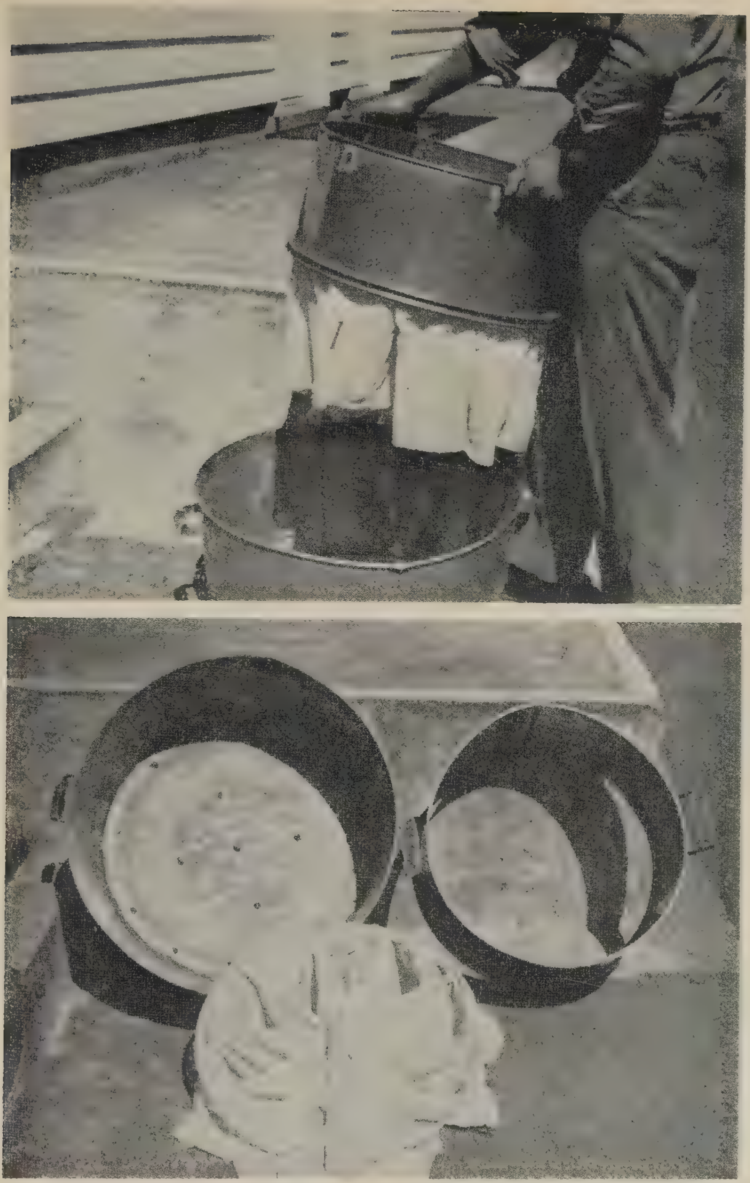

FIGURE 2.—Ten-part sampling net used to obtain fish for marking and to estimate the numbers of marked and unmarked fish released.

3 and shown in figure 3. General sampling levels for each time-location stratum were predetermined; typically, about 20 percent of the catch is sampled for marks, and from 50 to 100 unmarked fish are sampled to obtain age, length, and weight.

Catch data for each time-location stratum are provided by the management agencies. For most fisheries, the catch of chinook salmon in numbers of fish is an estimate. Commercial catches are estimated either from the total weight of landings and an estimate of average fish size or from total salmon landings (numbers) and an estimate of species composition. Estimates of sport catches are from measures of total effort and catch per-unit-effort or from salmon punch cards (filled out by anglers) together with independent sampling by the management agency.

Because the catch of hatchery-reared fish depends on length and timing of the fishing seasons as well as on the numbers of fish available, an estimate of the numbers of hatchery fish which escape the fishery is required to measure the

Table 3.—*Areas where catches were examined for marked fall chinook salmon of Columbia River origin by port or zone of landing and type of fishery*

Area sampled	Type of fishery				
	Sport	Commercial			
	Rod and reel	Troll	Gill net	Dip net	Purse seine
Southeast Alaska		Zones 1, 3–15, 18, 22	Zones 1, 6, 8, 11, 15, 18, 19.		
British Columbia		Alaska area Zones 29, 40–43, Area C.	Zones 29, 40, 41–43		Zones 40–43
Washington ocean	Sekiu	Seattle	Juan de Fuca Strait.		
	Neah Bay	Neah Bay	Grays Harbor.		
	La Push	La Push	Willapa Bay.		
	Westport	Westport.			
	Ilwaco	Ilwaco.			
Puget Sound	Zones 6–12.				
Oregon ocean	Warrenton	Astoria.			
	Depoe Bay	Tillamook.			
	Newport	Nestucca.			
	Florence	Depoe Bay.			
	Reedsport	Newport.			
	Coos Bay	Florence.			
	Gold Beach	Reedsport.			
	Brookings	Coos Bay.			
		Port Orford.			
		Brookings.			
California ocean	Crescent City	Crescent City.			
	Eureka	Eureka.			
	Fort Bragg	Fort Bragg.			
	San Francisco	San Francisco.			
	Monterey	Monterey.			
Columbia River	Zones 1–5		Zones 1–6	Klickitat River.	

hatchery output. For this reason, plans for mark sampling also included examining the fish returning to the hatcheries and searching for marked fish on certain natural spawning grounds.

Fish returning to the hatcheries are counted and examined for marks. At each hatchery an effort is made to obtain data on age, length, and sex for 25 to 50 unmarked fish per week. In addition to searching for marks at the 12 participating hatcheries, returns to 5 other hatcheries (Abernathy, Speelyai, Toutle, Klaskanine, and Sandy; fig. 1) are also examined for marks.

To estimate natural spawning of hatchery-reared fish, surveys were conducted on hatchery streams as well as those adjacent to or near the hatcheries under study. These streams are Klickitat, Big White Salmon, Little White Salmon, Wind, Washougal, Kalama, Lewis, Elokomin, and Grays Rivers and Plympton and Big Creeks. These surveys were designed to estimate size of the total spawning population, as well as to sample for marks, age, and length.

All data collected during the recovery phase of the study are recorded on a standard form (fig. 4). Data on a group of fish examined for marks are recorded according to the format along the upper part of the form; data for individual marked recoveries are recorded on the same form according to the format along the lower part. A scale sample from each marked fish is sent along with the form to the Fish Commission of Oregon's mark processing center, where the age is determined and entered on the form.[4] Samples of individual unmarked fish are recorded and processed in the same way as the marked fish.

After appropriate coding (e.g., type of mark, fishery and gear, and port of landing) the data are transferred to data processing cards from which tabulations are made. The tabulations are then forwarded to the Biometrics Unit at the Bureau of Commercial Fisheries Biological Laboratory, Seattle, Wash., where they are collated with catch information, and a summary report of each year's sampling effort is assembled.

SOURCES OF VARIATION

Two major sources of variation in the contribution of hatcheries are being considered. The first is the variation from year to year, which is the reason for extending the marking experiment over four brood years. The second source of variation is among hatcheries. To examine this, a group of fish at each of the four hatcheries was marked with a unique fin clip each year. Spring Creek and Kalama Hatcheries were allotted a special mark each year, and two additional special marks were rotated among eight of the remaining hatcheries so all hatcheries, except two, received special

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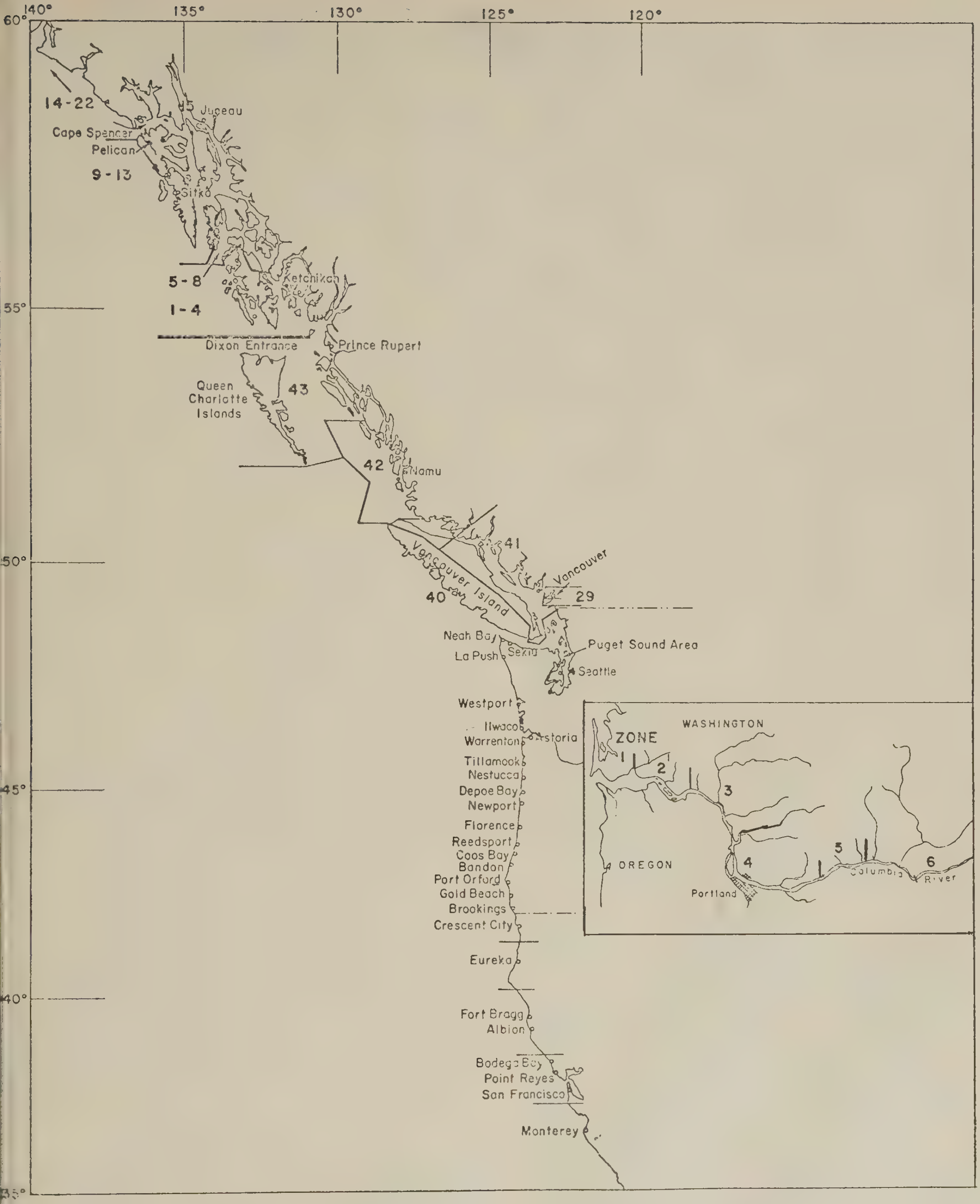
[4] In some instances (British Columbia and Washington fisheries), ages are determined by the agency that collects the data.


140°
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45°
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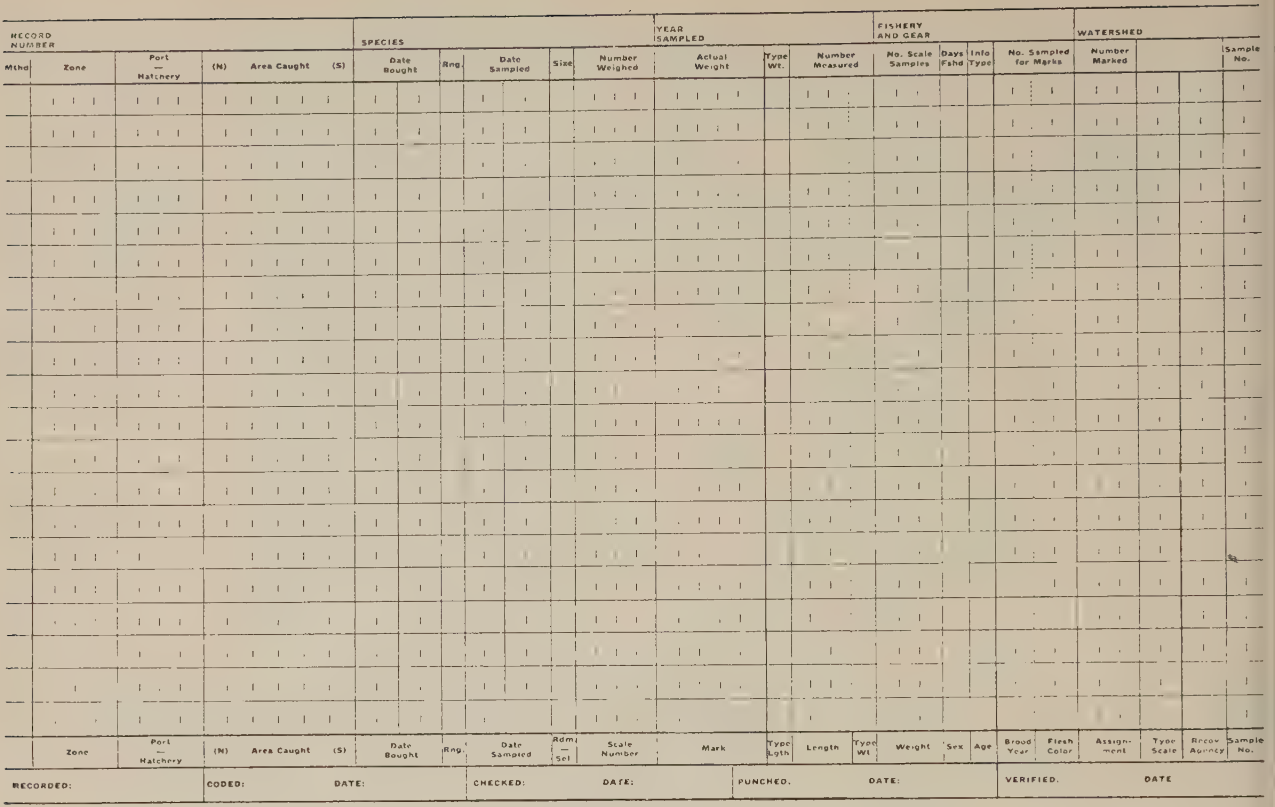
14-22
Juneau
Cape Spencer
Pelican
9-13
Sitka
5-8
Ketchikan
1-4
Dixon Entrance
Prince Rupert
Queen Charlotte Islands
43
42
Namu
41
Vancouver
29
Vancouver Island
40
Neah Bay
La Push
Sekiu
Puget Sound Area
Seattle
Westport
Ilwaco
Warrenton
Astoria
Tillamook
Nestucca
Depoe Bay
Newport
Florence
Reedsport
Coos Bay
Bandon
Port Orford
Gold Beach
Brookings
Crescent City
Eureka
Fort Bragg
Albion
Bodega Bay
Point Reyes
San Francisco
Monterey
WASHINGTON
ZONE
1
2
3
OREGON
4
5
6
Portland
Columbia River

Figure 3.—Ports and zones sampled for marked fall chinook salmon of Columbia River origin.



RECORD NUMBER | SPECIES | YEAR SAMPLED | FISHERY AND GEAR | WATERSHED

Mthd | Zone | Port — Hatchery | (N) Area Caught (S) | Date Bought | Rng | Date Sampled | Size | Number Weighed | Actual Weight | Type Wt. | Number Measured | No. Scale Samples | Days Fshd | Info Type | No. Sampled for Marks | Number Marked | Sample No.

Zone | Port — Hatchery | (N) Area Caught (S) | Date Bought | Rng. | Date Sampled | Rdm — Sel | Scale Number | Mark | Type Lgth | Length | Type Wt | Weight | Sex | Age | Brood Year | Flesh Color | Assignment | Type Scale | Recov Agency | Sample No.

RECORDED: | CODED: | DATE: | CHECKED: | DATE: | PUNCHED. | DATE: | VERIFIED. | DATE

FIGURE 4.—Form for recording mark recoveries and biological data.

marks. Marks selected were the excised right or left ventral fin, with and without the adipose fin. In addition, part of the left maxillary bone was removed in the even numbered brood years and part of the right maxillary in odd numbered brood years. These marks, together with the hatcheries involved and expected age of appearance in the sampling area, are shown in table 2.

Procedures for selecting fish, marking them, and sampling them at release to estimate mark ratios were the same as described earlier for the common (adipose-maxillary) mark.

Certain items of information concerning the rearing history were collected at each hatchery to explain some of the expected variations in contribution between hatcheries and between years. This information included numbers of adults spawned, incidence of disease in adults,, mortalities during incubation of eggs and rearing of young, incidence and treatment of disease in progeny, diet, fish size at release, and water temperatures during incubation, rearing, and at the release site.

For the same purpose, groups of marked and unmarked fish obtained at time of release from each hatchery underwent numerous tests at Abernathy Salmon Cultural Laboratory. Variables of interest included physical capabilities, body composition, hematology, and pathology. Physical capability of each group of fish was indexed by use of a stamina tunnel; body composition of protein, lipid, ash, water and glycogen was determined by proximate analyses; hematology consisted of hematocrit determinations and chemical measurements of blood plasma to determine levels of calcium, phosphorus, chloride, glucose, protein, albumin, cholesterol, icteric index, creatinine, uric acid, ammonia, and urea; and pathology included examinations for disease organisms from which a "disease index" was determined.

ESTIMATING PROCEDURES

The contribution (catch) of hatchery-reared fish will be estimated, as noted earlier, from data on the proportion of hatchery fish that were marked (or expected marked to unmarked ratio), the chinook salmon catch by time period within a season for a particular fishery, the number of fish examined for marks, and the number of marked fish recovered. In addition to obtaining an estimate of the catch of a given age group of hatchery fish, we are estimating the percentage contribution of hatchery fish to the total catch of that age group. This makes it necessary to subdivide the catch by age group on the basis of an estimated age composition.

For a particular fishery (e.g., Washington ocean sport fishery at Westport) let:

c_i = catch during ith period

n_i = number of fish examined for marks during ith period

n_{ijk} = number of marked fish with the kth kind of mark and of the jth age group recovered during the ith period

p_{ijk} = proportion of n_i having kth kind of mark and of the jth age group $= n_{ijk}/n_i$

Then an estimate of the catch of fish with the kth kind of mark and of the jth age group for the ith period is:

$$m_{ijk} = p_{ijk} c_i \qquad (1)$$

An estimate of the catch of all marked fish of the jth age group for the ith period is:

$$m_{ij.} = c_i \sum_k p_{ijk} = \sum_k m_{ijk}$$

and an estimate of the catch of all marked fish of all age groups for the ith period is:

$$m_{i..} = \sum_j m_{ij.}$$

The estimated catch of unmarked fish during the ith period is then:

$$u_i = c_i - m_{i..}$$

If g_{ij} is the proportion of the sample of unmarked fish belonging to the jth age group for the ith period, then an estimate of the catch of unmarked fish of the jth age group for the ith period is:

$$u_{ij} = g_{ij} u_i$$

Hence, the estimate of the total catch (marked and unmarked) of the jth age group for the ith period is:

$$c_{ij} = u_{ij} + m_{ij.}$$

and the estimated seasonal catch of marked and unmarked fish of the jth age group is:

$$c_{.j} = \sum_i c_{ij} \qquad (2)$$

Now, if we designate a particular hatchery evaluation mark (e.g., adipose-right maxillary) by setting k=1 in equation (1), then an estimate of the seasonal catch of Columbia River hatchery fish of the jth age group having that mark is:

$$m_{.j1} = \sum_i p_{ij1} c_i \qquad (3)$$

If, for example, we are interested in marked hatchery fish (adipose-right maxillary mark) of the 1961 brood, then their estimated catch in 1963 as 2-year-old fish is:

$${}_3m_{.21} = \sum_i ({}_3p_{i21})\ ({}_3c_i)$$

where the presubscript denotes the last digit of the sampling year. Similarly, the estimated catch in 1964 as 3-year-old fish is:

$${}_4m_{.31} = \sum_i ({}_4p_{i31})\ ({}_4c_i)$$

and the estimated catch in 1965 as 4-year-old fish is:

$${}_5m_{.41} = \sum_i ({}_5p_{i41})\ ({}_5c_i)$$

and similarly for still later years of capture.

An approximate variance estimate for $m_{.j1}$ is:

$$V(m_{.j1}) = C^2 \sum_i (w^2_i p_{ij1}/n_i) + V(C) \left[\left(\sum_i w_i p_{ij1}\right)^2 - \sum_i w^2_i p_{ij1}/n_i \right] \qquad (4)$$

where $C = \sum_i c_i$, $w_i = c_i/C$ and $V(C)$ is the variance of the estimated seasonal catch. If the catch, C, is known, then only the first item in (4) contributes to the variance estimate.

Now if ${}_ar_{j1}$ is the expected proportion of Columbia River hatchery fish of the jth age group in sampling year "a," which is marked with a particular mark (e.g., let k=1 for adipose–right maxillary), then an estimate of the seasonal catch of hatchery fish (marked and unmarked) of the jth age group in sampling year "a" is (from equation 3):

$${}_aH_j = {}_am_{.j1}/{}_ar_{j1} \qquad (5)$$

Hence, if, as in the example above, we are interested in the contribution of the 1961–brood hatchery fish, then an estimate of their catch (marked and unmarked) in 1963 as 2-year-old fish is:

$${}_3H_2 = {}_3m_{.21}/{}_3r_{21}$$

Likewise then, the estimated catch in 1964 as 3-year-old fish is:

$${}_4H_3 = {}_4m_{.31}/{}_4r_{31}$$

and similarly for the 1965 and 1966 sampling years.

An alternative procedure for estimating the seasonal catch of hatchery fish of the jth age group in sampling year "a" is:

$$ {}_aH_j = ({}_aM_{.j1}/{}_aq_{j1}) + \sum_{k=1}^{5} {}_aM_{.jk} \qquad (6) $$

where ${}_aq_{j1}$ is the expected marked (adipose-right maxillary) to unmarked ratio. The first term in this equation is an estimate of the catch of unmarked hatchery fish, and the second term is the estimated total catch of marked hatchery fish (summed over the five marks identifying hatchery fish).

The percent contribution of hatchery fish to the catch of the j^{th} age group in year "a" is then (from equation 2): ${}_aP_j = 100({}_aH_j/{}_ac_{.j})$.

Equations (5) and (6) are the basic equations for estimating the catch of Columbia River hatchery-reared fall chinook salmon of a given age in a given year. The numerator, ${}_aM_{.j1}$, in equation (5) is the estimated number of marked fish (adipose–right maxillary) in the catch at a particular fishery-port combination. As stated before, the denominator, ${}_ar_{j1}$, is the expected proportion that ${}_aM_{.j1}$ is of the total catch of hatchery fish of the same age group. Granting certain assumptions (set forth in the following section), the proportion of adipose-right maxillary marked fish in the hatchery releases is an estimate of ${}_ar_{j1}$. Hence, if r is the proportion of marked fish in the 1961 brood hatchery releases, we set

$$ {}_3r_{21} = {}_4r_{31} = {}_5r_{41} = {}_6r_{51} = r $$

So, we assume that the expected proportions of marked age 2 hatchery fish in 1963, age 3 fish in 1964, etc. are identical and equal to the proportion of marked fish in the releases of the 1961 brood hatchery fish.

The estimated proportion of marked fish in the total release of each brood year from the 12 hatcheries is based on estimates of the proportion of marked fish in the release and the size of release at each of the hatcheries. These latter estimates were obtained from a sampling procedure at the time of release at each of the hatcheries. If N_0 is the total number of fish released from a hatchery, then the number of fish removed by the sampling device at the first stage of sampling is:

$$ N_1 = s_1 N_0 $$

where s_1 is the actual proportion of the total number of fish removed by the sampling device. These fish, N_1, were then sampled again. If s_2 is the actual proportion of the total number of fish, N_1, removed by the sampling device during the second stage of sampling, then the number of fish which comprise the final sample is:

$$ N_2 = s_2 N_1 = s_2 s_1 N_0 $$

Hence, if s is an estimate of the proportion of fish removed by the sampler during a single stage (i.e., s is an estimate of both s_1 and s_2), then an estimate of the numbers of fish released, N_0, is:

$$ N = N_2/s^2 $$

The estimated proportion of fish removed by the sampling device was obtained from a number of trials using known numbers of fish, and the number of fish removed by the sampling device, N_2, was counted and sorted into the marked and unmarked groups. Thus, if M is the count of marked fish, then the estimated proportion of marked fish in the release is simply:

$$ r = M/N_2 $$

If N_i and r_i are the above estimated quantities for the i^{th} hatchery, then the estimated proportion, r, of marked fish in the total release from all hatcheries is:

$$ r = \sum_i w_i r_i $$

where $w_i = N_i/\Sigma N_i$

An estimate of the marked to unmarked ratio for the hatchery releases is similarly obtained.

ASSUMPTIONS

Several assumptions are inherent in the foregoing method of estimating the contribution of hatchery-reared fall chinook salmon to the fisheries. Three basic assumptions are:

1. A marked fish is identifiable as a marked fish throughout its life.
2. All observed chinook salmon having the kind of mark used on the hatchery-reared fish are indeed hatchery fish.
3. Chinook salmon are correctly aged from scale examinations and information on size of fish and date of capture.

In addition, we assume that marked fish behave like the unmarked hatchery fish. In particular we must assume:

4. Marked and unmarked hatchery fish have the same survival rates and maturity schedules.
5. Marked and unmarked hatchery fish have the same ocean distribution and are equally vulnerable to the fisheries.

Finally, because part of all hatchery releases bear the same mark, we assume that:

6. Either the ocean distribution and timing of migration of fish from each of the hatcheries are the same or the same proportion of each hatchery's production is marked.

The appropriateness of the estimating procedures described above is obviously dependent upon the validity of these assumptions. For this reason, the results must be considered as preliminary until sufficient data are collected to judge their validity. For example, if marked and unmarked fish have different survival rates, then the marked to unmarked ratio in the hatchery release is not appropriate [in equation (6)] and some adjustment should be made. To test the assumptions, additional studies and data collections were incorporated within the design of the marking experiment.

In connection with the first assumption (permanence of fin marks), marked juvenile fish were held and periodically examined to determine degree of mark regeneration. Also, illustrated forms on which missing fins or parts of fins are shaded out provide information on the samplers' interpretation of marked fish (fig. 5).

To test the second assumption (origin of fish marked with hatchery marks), fish were examined for natural marks while being marked. In addition, the cooperating fishery agencies agreed not to use the combination of marks used in this study on any group of 1965–brood chinook salmon. This group will be sampled as 2-, 3-, and 4-year-old fish during the 1967, 1968, and 1969 sampling years. Any observed marks of the kind used in this study will be from the natural loss of fins.

A test of scale readers was designed to test the third assumption (accuracy of age assignments). Scales from 400 marked fish of known age were submitted to six readers from the Fisheries Research Board of Canada, Washington Department of Fisheries, Oregon Game Commission, Fish Commission of Oregon (two readers), and Bureau of Commercial Fisheries. Length of fish and date of capture were available for each scale.

The fourth assumption (equality of survival rates and maturity schedules) will be examined from data on a different type of mark applied to fish at one of the hatcheries. At Little White Salmon Hatchery, a fraction of the 1964 brood was marked with TM 50 (oxytetracycline) that was added to the diet. This mark was selected to identify a hatchery stock because it apparently does not affect their growth or survival (Weber and Ridgway, 1967). As a result, some of the fish are double marked—with a finclip and TM 50. Returns to the hatchery in 1966, 1967, 1968, and 1969 will be examined for changes since release in the proportion of TM 50 marked fish which also have the finclip. In addition to the TM 50 marking at this hatchery, data bearing on the changes in marked to unmarked ratios (i.e., finclip vs. totally unmarked) between release and return will be available from the returns to each of the participating hatcheries.

With the resources available, we could not test the fifth assumption (equality of ocean distribution and vulnerability). Indirect evidence may be obtained, however, by comparing the ocean distribution of marked fish with the distribution as determined by past tagging experiments in the ocean.

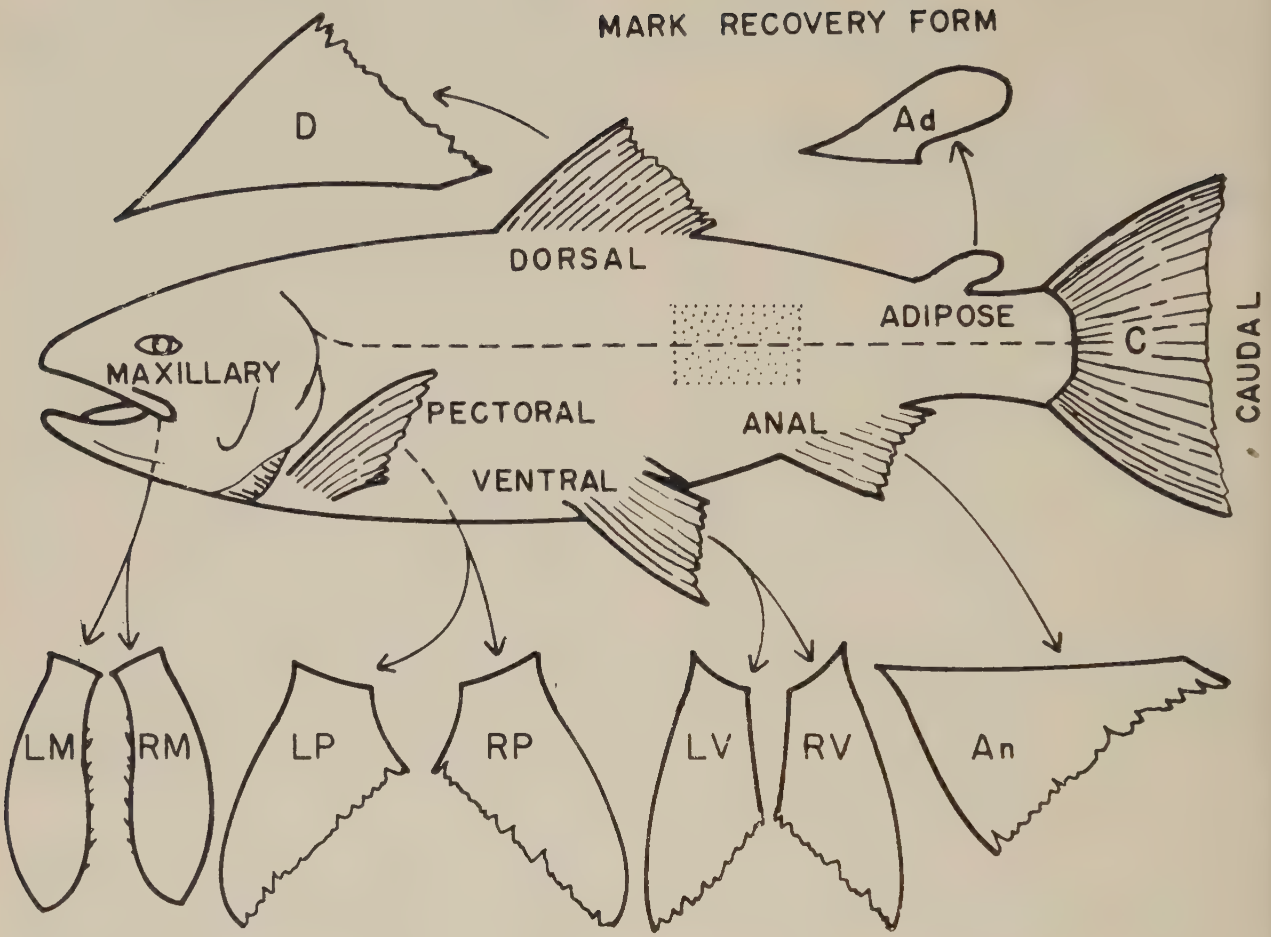
The sixth assumption (equality of ocean distribution or proportion marked among hatcheries) will be examined from data collected in that part of the study designed to examine the variations in contribution between hatcheries and, of course, from the data collected from each hatchery at the time of release.

RELEASES OF FISH

The marking phase of the hatchery contribution study (concluded in 1965) included marking a portion of the fall chinook production of each of the 12 hatcheries with the same mark; marking a portion of the production of 4 hatcheries with a unique mark; measuring the quality of marking; examining hatchery fish for naturally missing fins; and obtaining samples of fish to determine regeneration of marks and for measuring certain physical and physiological characteristics of the releases for each of the brood years. Analyses of these latter data in terms of explaining

AGENCY:

SCALE ENVELOPE NO.



COMMENTS:

FIGURE 5.—Form for recording type of mark observed.

sources of variation must await completion of the study.

Table 4 shows for each mark type and brood year the estimated numbers of chinook salmon released and the proportions of fish that were marked, and ratios of marked-to-unmarked fish. Detailed data for each hatchery are given in appendix tables 1, 2, 3, and 4.

During the 4 years of marking (i.e., 1961-64 broods), 213 million fall chinook salmon were released from the hatcheries under study. Included were 21.3 million fish with the adipose-maxillary mark. This mark, common to all of the 12 hatcheries, was 9.9 to 10.1 percent of the releases. In addition, the release included 9.6 million fish with special marks unique to individual hatcheries. These special marks were 9.1 to 30.5 percent of the yearly releases from the hatcheries where used.

Samples of over 100,000 marked fish were examined each year and graded according to quality of mark. A score of 5 was assigned for a good mark, 3 for an acceptable mark, and 0 for an unacceptable mark. Average scores were 4.9, 4.9, 4.9, and 4.8 for 1961, 1962, 1963, and 1964 broods, respectively. The lowest average score for any hatchery-mark type combination was 4.1; all remaining scores were greater than 4.5. Although a certain

TABLE 4.—*Estimated numbers and mark ratios of fall chinook salmon released from study hatcheries for 1961–64 brood years*

Brood year	Mark	Origin of mark	Marked release	Marked and unmarked release	Marked/ Marked and unmarked	Marked/ unmarked
			Number	*Number*		
1961	Ad-RM	All hatcheries	5, 446, 439	53, 653, 214	0. 1015	0. 1193
1962	Ad-LM	do	5, 249, 079	52, 470, 003	. 1000	. 1163
1963	Ad-RM	do	5, 986, 464	60, 112, 063	. 0996	. 1155
1964	Ad-LM	do	4, 638, 237	46, 778, 552	. 0992	. 1175
		Subtotal	21, 320, 219	213, 013, 832		
1961	Ad-LV-RM	Spring Creek	1, 133, 019	10, 925, 933	. 1037	. 1308
	Ad-RV-RM	Kalama	475, 964	4, 906, 845	. 0970	. 1210
	LV-RM	Elokomin	480, 533	1, 575, 000	. 3051	. 5075
	RV-RM	Oxbow	450, 446	4, 549, 959	. 0990	. 1241
1962	Ad-LV-LM	Spring Creek	866, 892	8, 408, 267	. 1031	. 1299
	Ad-RV-LM	Kalama	437, 669	4, 599, 326	. 0952	. 1173
	LV-LM	Grays	241, 494	1, 359, 761	. 1776	. 2437
	RV-LM	Cascade	541, 158	4, 217, 910	. 1283	. 1667
1963	Ad-LV-RM	Spring Creek	751, 243	7, 467, 629	. 1006	. 1264
	Ad-RV-RM	Kalama	456, 158	4, 883, 937	. 0934	. 1156
	LV-RM	Klickitat	521, 610	2, 888, 208	. 1806	. 2501
	RV-RM	Big Creek	579, 967	1, 985, 838	. 2920	. 4770
1964	Ad-LV-LM	Spring Creek	600, 953	6, 554, 455	. 0917	. 1139
	Ad-RV-LM	Kalama	319, 412	3, 496, 560	. 0914	. 1129
	LV-LM	Bonneville	957, 110	9, 887, 575	. 0968	. 1205
	RV-LM	Little White Salmon	797, 345	8, 365, 579	. 0953	. 1184
		Subtotal	9, 610, 973			
		Total	30, 931, 192			

amount of subjectivity is inherent in such a scoring system, these values indicate that a high quality was attained.

During the marking, over 30 million fingerlings were examined for naturally missing adipose and ventral fins. A total of 156 missing adipose and 201 missing ventral fins were observed. Although insignificant in relation to the fish examined, these numbers represent the frequency of naturally missing fins for these hatchery-reared fish only. A more direct measure of this source of error (i.e., occurrence of natural marks) in the hatchery contribution study will be possible during the years when fish of the 1965 brood are in the fishery. The marks used in the study were not applied to the 1965 brood.

Marked fingerlings obtained at time of release from the hatcheries were held in salt-water rearing ponds at Bowman Bay, Wash., for as long as 34 months. Periodic examinations were made to determine the extent of regeneration of the fin and maxillary marks, and the results are summarized in table 5.

Regeneration of the adipose mark was not apparent. Similarly, complete regeneration of the ventral mark did not occur. Some regeneration of the ventral mark, however, was apparent for a substantial portion of the fish in each group (up to 47 percent). In most cases, the ventral fin regenerated to less than 25 percent of its original size (as judged by the size of the paired ventral

TABLE 5.—*Regeneration of adipose fin, maxillary bone and ventral fin in test lots of fish, 1961–64 brood years, held at Bowman Bay, Wash.*

Adipose fin

Brood year	Age	Fish examined	Regeneration	
	Months	*Number*	*Number*	*Percent*
1961	20	115	0	0
1962	12	626	0	0
	23	452	0	0
	29	381	0	0
1963	12	872	0	0
	17	551	0	0
	26	371	0	0
	34	311	0	0
1964	14	416	0	0
	27	312	0	0

Maxillary bone

Brood year	Age	Fish examined	Complete regeneration	
	Months	*Number*	*Number*	*Percent*
1961	20	291	20	6. 9
1962	12	1, 079	32	3. 0
	23	734	38	5. 2
	29	652	76	11. 6
1963	12	1, 615	8	. 5
	17	1, 160	25	2. 2
	26	774	26	3. 4
	34	664	22	3. 3
1964	14	751	12	1. 6
	27	567	5	. 9

Ventral fin

Brood year	Age	Fish examined	Regeneration			
			Less than 25 percent		Greater than 25 percent	
	Months	*Number*	*Number*	*Percent*	*Number*	*Percent*
1961	20	291	116	39. 9	[1] 14	4. 8
1962	12	1, 079	444	41. 1	64	5. 9
	23	734	293	39. 9	37	5. 0
	29	652	247	37. 9	39	6. 0
1963	12	1, 615	559	34. 6	(2)	
	17	1, 160	408	35. 2	62	5. 3
	26	774	310	40. 0	41	5. 3
	34	664	182	27. 4	33	5. 0
1964	14	575	211	36. 7	22	3. 8
	27	432	86	19. 9	16	3. 7

[1] Complete regeneration did not occur in any of the groups.
[2] Degree of regeneration was not determined.

fin). Even where the regeneration was greater (up to 6 percent of the fish examined), the marks were readily identifiable owing to a deformation of the fin rays.

The maxillary mark completely regenerated for varying proportions of the groups examined. The relatively high occurrence of regeneration for the 1961- and 1962-brood fish (6.9–11.6 percent) was the basis for removing more of the maxillary bone for the next 2 brood years. Only the tip of the maxillary was removed for the 1961 and 1962 broods. For the 1963 and 1964 broods, the maxillary was excised at a point below the middle of the eye. This change in marking procedure is reflected in the smaller percentages of fish with regeneration (1–3 percent) for the 1963 and 1964-brood fish.

It is likely that these test fish were examined in greater detail and under better conditions than can be expected in actual sampling. The results of the examinations, however, make it doubtful that fin regeneration is an important source of error in the total program. Maxillary regeneration causes some difficulties and will be considered in a later section.

MARK RECOVERIES AND ESTIMATED CATCH OF MARKED FISH

The mark-sampling phase of the program began in 1963 when the 1961-brood-year fish first entered some of the fisheries as 2-year-olds. During the first year, sampling was limited to the Washington and Oregon ocean fisheries, Columbia River fisheries, and hatchery returns. Beginning in 1964, sampling was expanded to include most chinook salmon fisheries from Monterey, Calif., to and including southeast Alaska. The results reported here concern recoveries of the 1961 brood in 1963, 1964, 1965, and 1966. Recoveries from this brood in 1967 were minor.

The total catches of chinook salmon in the fisheries that were sampled and numbers of fish examined each year for marks and for age are given in table 6. Over the 4 years of sampling, 23 percent of the catch of 8.5 million fish were examined for marks. In addition, 1.5 percent of the total catch was sampled for age determinations and other data (e.g., length and weight). Mark sampling percentages were 28.3, 26.6, 19.8, and 21.5 percent for 1963, 1964, 1965, and 1966, respectively.

TABLE 6.—*Catches of chinook salmon and number of fish examined for marks and age, 1963–66*

Year	Catch [1] chinook salmon		Sampled for marks	Sampled for age
	1961 brood	All ages		
	Number of fish			
1963	41, 786	570, 172	161, 460	20, 000
1964	1, 565, 549	2, 671, 976	709, 660	33, 000
1965	998, 849	2, 572, 919	508, 730	34, 000
1966	206, 765	2, 645, 537	569, 265	40, 000
Total	2, 812, 949	8, 460, 604	1, 949, 115	127, 000

[1] Total catch is only for those fisheries sampled.

RECOVERIES OF MARKED FISH

Table 7 summarizes all marks of possible Columbia River hatchery origin (1961 brood year) recovered in the fisheries. Included in the table are recoveries of marks that could be the result of maxillary regeneration. A total of 9,573 marked fish of possible Columbia River hatchery origin were recovered during the 4 years of sampling. Although fairly large numbers of marked fish of the 1961 brood were recovered in 1966 and during the limited sampling in 1963, most of them were recovered as 3-year-old fish in 1964. Exceptions were the fish marked at Kalama Hatchery; slightly more of these fish were recovered in 1965 than in 1964.

The distribution of recoveries for each year by region of capture and type of fishery is shown in table 8. Only recoveries of the full marks are listed. The distribution of recoveries of the possible experimental marks was similar.

As 2-year-old fish, those with 1961-brood marks were recovered only in the Washington ocean sport and Columbia River gill net fisheries. Although many fisheries were not sampled in 1963, 2-year-old mark recoveries of the 1962- and 1963-brood fish indicate that the contribution of this age group to other fisheries is relatively minor. By 1964 the marked fish were distributed over the entire range of sampling. For ocean fisheries they appeared most frequently, however, in Washington and British Columbia catches (although not shown in table 8, the bulk of the British Columbia recoveries were from the troll fishery landings on the west coast of Vancouver Island). The distributions of recoveries in 1965 and 1966 were similar to 1964 but in fewer numbers.

The distributions of marked fish that originated from Spring Creek and Kalama Hatcheries were different. Proportionately more of the Kalama

TABLE 7.—*Marked 1961 brood-year chinook salmon of possible Columbia River hatchery origin recovered in the fisheries, 1963–66*

Origin of mark	Mark	Year of capture				Total
		1963	1964	1965	1966	
		Number of fish				
All hatcheries	Ad-RM	110	4, 145	1, 885	144	6, 284
	Ad	79	561	189	30	859
Spring Creek	Ad-LV-RM	29	861	270	5	1, 165
	Ad-LV	19	125	42	2	188
Kalama	Ad-RV-RM	5	248	268	64	585
	Ad-RV	1	17	35	5	58
Elokomin	LV-RM	0	38	18	2	58
	LV	3	75	57	21	156
Oxbow	RV-RM	3	54	16	5	78
	RV	3	65	55	24	147
Total		252	6, 189	2, 835	302	9, 578

marks were recovered in the northern portions of the sampling range. For example in 1964, 3.3 times as many Kalama marks were recovered in the British Columbia troll fishery than were recovered in the Washington troll fishery. Such a comparison for Spring Creek marks shows a figure of 1.3 times. Moreover, Kalama marked fish were the only ones with marks (specific to a hatchery) recovered in the southeast Alaska fisheries.

Distributions of recoveries of marked fish that originated from Elokomin and Oxbow Hatcheries were similar to the distribution of Spring Creek recoveries, but the number of marks recovered was much smaller.

Recoveries of marked fall chinook salmon of the 1961 brood from the Columbia River escapement are presented in appendix table 5 and summarized in table 9. As in the ocean fisheries, most of the recoveries at the hatcheries were made in 1964. The exception was the relatively high 1965 recovery of marks originating from Kalama Hatchery.

Mark recoveries at hatcheries were obtained from examination of the entire hatchery returns. Therefore, it is impossible to make meaningful comparisons between hatchery recoveries and recoveries in tributary streams and fisheries, where only a portion of the populations was examined for marks.

ESTIMATED CATCHES OF MARKED FISH

As shown by equation (3), the total catch of fish with a particular mark is estimated for each stratum (fishery, port of landing or area of capture, and time period) from the catch and the proportion of fish having the mark in the catch sample. (It is assumed that a random sample is examined for marked fish and that all marked fish are observed.) The annual catch of fish with a particular mark is estimated for each fishery category (e.g., Washington troll fishery) by summing over the time periods and appropriate ports of landing

TABLE 8.—*Marked 1961-brood Columbia River chinook salmon recovered by year, region of capture, and type of fishery, 1963–66*

Origin and type of mark	Year	California		Oregon		Washington			Puget Sound	British Columbia			S.E. Alaska		Columbia River		
							Commercial						Commercial			Commercial	
		Sport [1]	Commercial [2]	Sport	Commercial	Sport	Troll	Gill net	Sport	Troll	Gill net	Purse seine	Troll	Gill net	Sport	Gill net	Dip net
		Number of recoveries															
All hatcheries (Ad-RM).	1963	(*)	(*)	0	0	88	0	(*)	(*)	(*)	(*)	(*)	(*)	(*)	0	22	(*)
	1964	0	4	18	102	389	1, 057	2	(*)	1, 654	1	1	0	0	1	880	36
	1965	0	0	7	6	91	128	3	0	505	1	0	2	0	0	1, 106	6
	1966	0	1	0	0	13	14	0	0	63	0	(*)	0	(*)	0	53	0
Spring Creek (Ad-LV-RM).	1963	(*)	(*)	0	0	23	0	(*)	(*)	(*)	(*)	(*)	(*)	(*)	0	6	(*)
	1964	0	3	1	31	81	246	0	(*)	321	0	0	0	0	0	178	0
	1965	0	0	0	2	12	21	1	0	41	0	0	0	0	0	193	0
	1966	0	0	0	0	0	0	0	0	2	0	(*)	0	(*)	0	3	0
Kalama (Ad-RV-RM).	1963	(*)	(*)	0	0	5	0	(*)	(*)	(*)	(*)	(*)	(*)	(*)	0	0	(*)
	1964	0	1	0	7	20	49	0	(*)	161	0	0	1	0	0	9	0
	1965	0	0	0	2	14	35	1	0	104	0	0	5	0	0	107	0
	1966	0	0	0	0	1	4	0	0	24	0	(*)	2	(*)	0	33	0
Elokomin (LV-RM).	1963	(*)	(*)	0	0	0	0	(*)	(*)	(*)	(*)	(*)	(*)	(*)	0	0	(*)
	1964	0	1	1	4	3	14	0	(*)	12	0	0	0	0	0	3	0
	1965	0	0	0	2	3	2	0	0	2	0	0	0	0	0	9	0
	1966	0	0	0	0	0	1	0	0	1	0	(*)	0	(*)	0	0	0
Oxbow (RV-RM).	1963	(*)	(*)	0	0	3	0	(*)	(*)	(*)	(*)	(*)	(*)	(*)	0	0	(*)
	1964	0	0	2	9	8	23	0	(*)	4	0	0	0	0	0	8	0
	1965	1	0	1	1	0	3	0	0	7	0	0	0	0	2	1	0
	1966	0	0	0	0	2	0	0	0	1	0	(*)	0	(*)	0	2	0

*No sampling.

[1] All sport fishing is by rod and reel.

[2] Unless otherwise noted commercial fishing is by trolling.

TABLE 9.—*Recoveries of 1961-brood fall chinook salmon in the Columbia River escapement by type of mark, recovery location, and year of capture, 1963–66*

Origin of mark	Mark	Recovery location [1]											
		Study hatcheries				Other hatcheries				Tributary streams			
		1963	1964	1965	1966	1963	1964	1965	1966	1963	1964	1965	1966
		Numbers of recoveries											
All hatcheries	Ad–RM	100	1,296	679	57	(*)	4	1	0	(*)	53	104	9
	Ad	24	215	167	2	(*)	0	0	0	(*)	11	5	0
Spring Creek	Ad–LV–RM	41	364	121	1	(*)	0	0	0	(*)	1	1	0
	Ad–LV	5	51	23	1	(*)	0	0	0	(*)	0	0	0
Kalama	Ad–RV–RM	0	8	112	38	(*)	5	0	0	(*)	0	15	4
	Ad–RV	0	0	4	0	(*)	0	0	0	(*)	0	1	1
Elokomin	LV–RM	2	4	1	0	(*)	0	0	0	(*)	4	1	0
	LV	0	8	5	0	(*)	2	2	0	(*)	0	0	1
Oxbow	RV–RM	4	52	22	1	(*)	0	0	0	(*)	0	0	0
	RV	3	7	10	0	(*)	0	0	0	(*)	0	0	0
Total		179	2,005	1,144	100	(*)	11	3	0	(*)	69	127	15

*Not sampled.

[1] The "study hatcheries" include the 12 hatcheries participating in the marking program. "Other hatcheries" include Abernathy, Speelyai, Toutle, Klaskanine, and Sandy Hatcheries. "Tributary streams" include those tributaries listed in an earlier section.

(or area of capture). The same system is used to estimate the total number of marked fish in spawning populations of tributary streams.

Estimated numbers of marked 1961-brood fish caught in the fisheries, returning to the hatcheries and escaping to tributary streams, are listed in table 10. Estimated numbers include fish which had a partial mark only—not a complete double or triple mark—(e.g., Ad only instead of Ad–RM or Ad–LV only instead of Ad–LV–RM). These numbers are substantial—for example, we estimated that the fisheries took 2,710 adipose-only marked fish or about 14 percent of the number with the full mark (Ad–RM).

The partial marks were from naturally marked fish, from experimentally marked fish with complete regeneration of the maxillary mark, or possibly both. From the mark regeneration experiment described earlier, we expected complete regeneration of the maxillary mark for about 12 percent of the marked fish over a 2.5-year period. To determine if the percentages observed can be explained by the expected regeneration of the maxillary mark, it is necessary to make a detailed

TABLE 10.—*Estimated number of marked fall chinook salmon of 1961 brood in catches, tributary spawning populations, and hatchery returns by type of mark, region of recovery, type of fishery, and year of capture, 1963–66*

Region	Fishery type	Ad–RM				Ad				Total			
		1963	1964	1965	1966	1963	1964	1965	1966	1963	1964	1965	1966
		Number of fish											
Ocean fisheries:													
Southeastern Alaska	Commercial	(*)	0	7	0	(*)	2	23	2	(*)	2	30	2
British Columbia	do	(*)	4,106	1,871	235	(*)	566	370	68	(*)	4,672	2,241	303
Washington	Sport	375	1,681	416	67	196	224	104	15	571	1,905	520	82
	Commercial	0	3,241	455	41	3	397	59	8	3	3,638	514	49
Oregon	Sport	0	72	26	0	0	93	16	0	0	165	42	0
	Commercial	0	324	10	0	0	45	12	0	0	369	22	0
California	Sport	(*)	0	0	0	(*)	0	0	0	(*)	0	0	0
	Commercial	(*)	23	0	6	(*)	0	4	0	(*)	23	4	6
Subtotal	Sport	375	1,753	442	67	196	317	120	15	571	2,070	562	82
	Commercial [1]	0	7,694	2,343	282	3	1,010	468	78	3	8,704	2,811	360
Columbia River fisheries	Sport	0	7	0	0	0	14	0	0	0	21	0	0
	Commercial [2]	72	2,151	3,544	176	76	297	92	24	148	2,448	3,636	200
Total	All fisheries	447	11,605	6,329	525	275	1,638	680	117	722	13,243	7,009	642
Columbia River escapement:													
Study hatcheries	(3)	100	1,296	679	57	24	215	167	2	124	1,511	846	59
Other hatcheries	(4)	(*)	4	1	0	(*)	0	0	0	(*)	4	1	0
Tributary streams		(*)	393	355	21	(*)	74	11	0	(*)	467	366	21
Total	Escapement	100	1,693	1,035	78	24	289	178	2	124	1,982	1,213	80

*Not sampled.

[1] Primarily troll fisheries.

[2] Primarily gill net.

[3] Twelve hatcheries participating in the marking program.

[4] Toutle, Abernathy, Speelyai, Sandy, and Klaskanine Hatcheries.

TABLE 10.—*Estimated number of marked fall chinook salmon of 1961 brood in catches, tributary spawning populations, and hatchery returns by type of mark, region of recovery, type of fishery, and year of capture, 1963–66*—Continued

Region	Fishery type	Ad–LV–RM (Spring Creek)				Ad–LV				Total			
		1963	1964	1965	1966	1963	1964	1965	1966	1963	1964	1965	1966
							Number of fish						
Ocean fisheries:													
Southeastern Alaska	Commercial	(*)	0	0	0	(*)	0	0	0	(*)	0	0	0
British Columbia	do	(*)	767	140	5	(*)	74	24	0	(*)	841	164	5
Washington	Sport	89	354	52	0	63	77	45	0	152	431	97	0
	Commercial	0	869	78	0	4	215	4	0	4	1,084	82	0
Oregon	Sport	0	5	0	0	4	44	4	0	4	49	4	0
	Commercial	0	73	16	0	0	8	4	0	0	81	20	0
California	Sport	(*)	0	0	0	(*)	0	0	0	(*)	0	0	0
	Commercial	(*)	15	0	0	(*)	10	0	0	(*)	25	0	0
Subtotal	Sport	89	359	52	0	67	121	49	0	156	480	101	0
	Commercial [1]	0	1,724	234	5	4	307	32	0	4	2,031	266	5
Columbia River fisheries	Sport	0	0	0	0	0	0	16	0	0	0	16	0
	Commercial [2]	19	453	608	10	3	65	61	7	22	518	669	17
Total	All fisheries	108	2,536	894	15	74	493	158	7	182	3,029	1,052	22
Columbia River escapement:													
Study hatcheries	(3)	41	364	121	2	5	51	23	1	46	415	144	3
Other hatcheries	(4)	(*)	0	0	0	(*)	0	0	0	(*)	0	0	0
Tributary streams		(*)	1	4	0	(*)	0	0	0	(*)	1	4	0
Total	Escapement	41	365	125	2	5	51	23	1	46	416	148	3

*Not sampled.

[1] Primarily troll fisheries.
[2] Primarily gill net.
[3] Twelve hatcheries participating in the marking program.
[4] Toutle, Abernathy, Speelyai, Sandy, and Klaskanine Hatcheries.

TABLE 10.—*Estimated number of marked fall chinook salmon of 1961 brood in catches, tributary spawning populations, and hatchery returns by type of mark, region of recovery, type of fishery, and year of capture, 1963–66*—Continued

Region	Fishery type	Ad–RV–RM (Kalama)				Ad–RV				Total			
		1963	1964	1965	1966	1963	1964	1965	1966	1963	1964	1965	1966
							Number of fish						
Ocean fisheries:													
Southeastern Alaska	Commercial	(*)	5	14	4	(*)	0	21	0	(*)	5	35	4
British Columbia	do	(*)	420	480	89	(*)	21	25	6	(*)	441	480	95
Washington	Sport	17	74	72	5	4	4	28	4	21	78	100	9
	Commercial	0	132	122	7	0	17	20	0	0	149	142	7
Oregon	Sport	0	0	0	0	0	0	0	0	0	0	0	0
	Commercial	0	18	4	0	0	3	0	0	0	21	4	0
California	Sport	(*)	0	0	0	(*)	0	0	0	(*)	0	0	0
	Commercial	(*)	2	0	0	(*)	0	0	0	(*)	2	0	0
Subtotal	Sport	17	74	72	5	4	4	28	4	21	78	100	9
	Commercial [1]	0	577	595	100	0	41	66	6	0	618	661	106
Columbia River fisheries	Sport	0	0	0	0	0	0	0	0	0	0	0	0
	Commercial [2]	0	32	377	106	0	6	22	5	0	38	399	111
Total	All fisheries	17	683	1,044	211	4	51	116	15	21	734	1,160	226
Columbia River escapement:													
Study hatcheries	(3)	0	8	112	38	0	0	4	0	0	8	116	38
Other hatcheries	(4)	(*)	5	0	0	(*)	0	0	0	(*)	5	0	0
Tributary streams		(*)	0	56	9	(*)	0	4	2	(*)	0	60	11
Total	Escapement	0	13	168	41	0	0	8	2	0	13	176	49

*Not sampled.
[1] Primarily troll fisheries.
[2] Primarily gill net.
[3] Twelve hatcheries participating in the marking program.
[4] Toutle, Abernathy, Speelyai, Sandy, and Klaskanine Hatcheries.

examination of the data on mark recoveries and accuracy of determining the age of fall chinook salmon.

In test readings of scales from marked chinook salmon of known age, six scale readers correctly aged (total age) 83 percent of the 400 test scales (Godfrey, Worlund, and Bilton, 1968). Table 11 shows the estimated and actual percentage age compositions of the 400 test scales. From the results of this test, it appears that in any one year scale readers can estimate reasonably well the numbers of partially marked fish of a given age (and, hence, brood-year).

A summary of partially marked fish is presented in table 12; the data resulted from the combination of years and general mark types (e.g., Ad–LV and

TABLE 10.—*Estimated number of marked fall chinook salmon of 1961 brood in catches, tributary spawning populations, and hatchery returns by type of mark, region of recovery, type of fishery, and year of capture, 1963–66*—Continued

Region	Fishery type	LV-RM (Elokomin)				LV				Total			
		1963	1964	1965	1966	1963	1964	1965	1966	1963	1964	1965	1966
		Number of fish											
Ocean fisheries:													
Southeastern Alaska	Commercial	(*)	0	0	0	(*)	4	51	15	(*)	4	51	15
British Columbia	do	(*)	28	7	6	(*)	60	46	63	(*)	88	53	69
Washington	Sport	0	8	15	0	12	55	27	0	12	63	42	0
	Commercial	0	45	5	3	0	64	22	10	0	109	27	13
Oregon	Sport	0	3	0	0	0	11	0	0	0	14	0	0
	Commercial	0	9	3	0	0	13	5	0	0	22	8	0
California	Sport	(*)	0	0	0	(*)	0	0	0	(*)	0	0	0
	Commercial	(*)	7	0	0	(*)	0	21	0	(*)	7	21	0
Subtotal	Sport	0	11	15	0	12	66	27	0	12	77	42	0
	Commercial [1]	0	89	15	9	0	141	145	88	0	230	160	97
Columbia River fisheries	Sport	0	0	0	0	0	0	0	0	0	0	0	0
	Commercial [2]	0	7	28	0	0	24	17	13	0	31	45	13
Total	All fisheries	0	107	58	9	12	231	189	101	12	338	247	110
Columbia River escapement:													
Study hatcheries	(3)	2	4	1	0	0	8	5	0	2	12	6	0
Other hatcheries	(4)	(*)	0	0	0	(*)	2	2	0	(*)	2	2	0
Tributary streams		(*)	5	2	0	(*)	0	0	2	(*)	5	2	2
Total	Escapement	2	9	3	0	0	10	7	2	2	19	10	2

*Not sampled.

[1] Primarily troll fisheries.

[2] Primarily gill net.

[3] Twelve hatcheries participating in the marking program.

[4] Toutle, Abernathy, Speelyai, Sandy, and Klaskanine Hatcheries.

TABLE 10.—*Estimated number of marked fall chinook salmon of 1961 brood in catches, tributary spawning populations, and hatchery returns by type of mark, region of recovery, type of fishery, and year of capture, 1963–66*—Continued

Region	Fishery type	RV—RM (Oxbow)				RV				Total			
		1963	1964	1965	1966	1963	1964	1965	1966	1963	1964	1965	1966
		Number of fish											
Ocean fisheries:													
Southeastern Alaska	Commercial	(*)	0	0	0	(*)	0	41	2	(*)	0	41	2
British Columbia	do	(*)	8	16	6	(*)	59	51	77	(*)	67	67	83
Washington	Sport	11	43	0	9	10	52	21	75	21	95	21	84
	Commercial	0	58	9	0	0	29	14	8	0	87	23	8
Oregon	Sport	0	18	4	0	0	5	9	0	0	23	13	0
	Commercial	0	20	2	0	0	21	1	0	0	41	3	0
California	Sport	8	0	2	--------	(*)	0	0	0	(*)	0	2	0
	Commercial	(*)	0	0	0	(*)	0	71	3	(*)	0	71	3
Subtotal	Sport	11	61	6	9	10	57	30	75	21	118	36	84
	Commercial [1]	0	86	27	6	0	109	178	90	0	195	205	96
Columbia River fisheries	Sport	0	0	17	0	0	0	8	0	0	0	25	0
	Commercial [2]	0	24	3	16	2	14	16	5	2	38	19	21
Total	All fisheries	11	171	53	31	12	180	232	170	23	351	285	201
Columbia River escapement:													
Study hatcheries	(3)	4	52	22	1	3	7	10	0	7	59	32	1
Other hatcheries	(4)	(*)	0	0	0	(*)	0	0	0	(*)	0	0	0
Tributary streams		(*)	0	0	0	(*)	0	0	0	(*)	0	0	0
Total	Escapement	4	52	22	1	3	7	10	0	7	59	32	1

*Not sampled.

[1] Primarily troll fisheries.

[2] Primarily gill net.

[3] Twelve hatcheries participating in the marking program.

[4] Toutle, Abernathy, Speelyai, Sandy, and Klaskanine Hatcheries.

Ad–RV were combined as were their corresponding full marks Ad–LV–RM and Ad–RV–RM). Under the hypothesis that the partial marks are primarily from maxillary regeneration, each entry is an estimate of percentage regeneration of the maxillary. For the returns to the hatcheries under study, the percentages of adipose-ventral and adipose-only marks (10.9 and 16.1) were similar to the expected magnitude of maxillary regeneration from the fin regeneration experiments. It is likely, therefore, that these partial marks in the hatchery returns were from maxillary regeneration. The same cause is not indicated for the ventral-only marks, which, in the hatchery returns, were about twice as numerous as expected.

If the percentage of partial marks in the ocean fisheries (compared with that observed for the hatchery returns) is generally high, then we

Table 11.—*Actual and estimated age composition of 400 test scales read by 6 scale readers*

Evaluation	Age composition (years)				
	2	3	4	5	6
	Percent				
Estimated	18.4	38.5	28.2	12.5	2.4
Actual	20.2	41.8	24.5	13.5	.0

would tend to reject the hypothesis that these marks are caused primarily by regeneration and conclude that many of these partial marks occurred naturally.

Because the Ad–RV and Ad–LV partial marks are double fin marks, we assume that their occurrence (in catch and hatchery returns) was primarily the result of maxillary regeneration. Hence, the data in the column Ad–EV of table 12 reflects the variability in rate of maxillary regeneration. When we compare the percent occurrence of Ad and EV marks with that of Ad–EV marks and the percentages of Ad and EV marks in the catches and at the hatcheries, the Ad mark appears to have been caused primarily by maxillary regeneration; and single RV or LV marks appear to have resulted from naturally marked fish in addition to maxillary regeneration.

In view of the above, we combined the estimated numbers of partially marked fish with their corresponding full mark for each mark type except for the LV and RV marks. On this basis the estimated numbers of marked fall chinook salmon of Columbia River hatchery origin in the catch and escapement are summarized in table 13.

Table 12.—*Recoveries of partially marked fish by region of capture, type of fishery, and type of mark, 1963–66*

Region	Fishery type	Partial mark [1]		
		Ad–EV[2]	Ad	EV
		Percent		
Ocean fisheries:				
Southeastern Alaska	Commercial	47.7	79.4	100.0
British Columbia	do	7.4	13.9	83.4
Washington	Sport	25.3	17.5	74.6
	Commercial	17.7	11.1	55.0
Oregon	Sport	91.2	52.6	50.0
	Commercial	11.9	14.6	54.0
California	Sport			0
	Commercial	37.0	12.1	93.1
Subtotal	All	15.8	14.6	74.9
Columbia River fisheries	All	10.3	7.8	51.0
Columbia River escapement:				
Study hatcheries		10.9	16.1	27.7
Other hatcheries		0	0	100.0
Tributary streams		7.9	10.0	22.0
Subtotal		10.6	14.5	29.5

[1] Data in table are ratios (average for all years) of estimated numbers of partial marks to estimated sum of partial marks and corresponding complete marks expressed in percent.

[2] EV signifies "either ventral." Marks of same general type are combined.

Table 13.—*Estimated catch and escapement of marked fall chinook salmon of Columbia River hatchery origin by area of recovery, 1963–66*

Recovery category	Type of mark				
	Ad–RM[1]	Ad-LV-RM[1] (Spring Creek)	Ad-RV-RM[1] (Kalama)	LV-RM (Elokomin)	RV-RM (Oxbow)
	Numbers of fish				
Ocean fisheries	15,163	3,043	1,593	139	206
Columbia River fisheries	6,453	1,242	548	35	60
Total fisheries	21,616	4,285	2,141	174	266
Total escapement	3,399	612	238	14	79

[1] Includes partially marked fish.

Of the 1961 brood released from the 12 hatcheries with Ad–RM mark, we estimated that 21,600 were caught by the various fisheries between 1963 and 1966. An additional 3,400 fish escaped the fisheries and returned to spawn. The catch to escapement ratio for the 12 hatcheries is, therefore, about 6:1. For the four hatcheries represented by the other marks, this ratio was 12:1, 9:1, 3:1, and 7:1 (Elokomin, Kalama, Oxbow, and Spring Creek Hatcheries, respectively).

The estimated catch of marked fish (Ad–RM) that originated from the 12 hatcheries relative to numbers released was 21,616/5,446,439 or 3.97 fish per 1,000 released. Considerable variation in contribution occurred between hatcheries. The catch per 1,000 fish released was 0.36, 4.50, 0.59, and 3.78 for Elokomin, Kalama, Oxbow, and Spring Creek Hatcheries, respectively. Values for Elokomin and Oxbow Hatcheries are undoubtedly too low—some of the partial marks must have resulted from maxillary regeneration. If we assume that all the partial marks actually originated from Elokomin and Oxbow Hatcheries, their respective contribution would have been 1.53 and 1.95 per 1,000 fish released. These contributions still would be only one-half of those for Kalama and Spring Creek Hatcheries.

Before proceeding with the estimate of total contribution (marked and unmarked) of hatchery-reared fish to the catch, we will consider the precision of the estimate of the total catch of marked fish.

Equation (4), which provides an approximation of the variance of the estimated number of marks in the catch, requires an estimate of the precision of the seasonal chinook catch for each of the fisheries. Such estimates are not published except in a few instances (e.g., California troll and Oregon ocean sport fisheries). Lacking this information, we have assumed that the seasonal chinook catches in each fishery (except for Alaska troll and the ocean gill net and purse seine fisheries) are estimated within 15 percent of the true value; i.e., the variance of the catch, $V(C)$, is such that one-half the width of the 95 percent confidence interval, $2[V(C)]^{1/2}$, is 15 percent of the estimated catch, C. We then have:

$$\begin{aligned} V(C) &= (0.5 \times 0.15 \times C)^2 \\ &= 0.0056\ C^2. \end{aligned}$$

Where available (e.g., California troll), estimates of the precision of the catches are well within the assumed value.

In the Alaska troll fishery and the ocean net fisheries, catches are reported in numbers of fish. The variance of the catch and, therefore, the second term in equation (4) is zero for each of these fisheries.

Substituting these values of $V(C)$ in equation (4) and summing over the strata (i.e., fisheries and years) gives 357,000; 26,000; 13,000; 1,100; and 2,300 as approximate variances for the estimated numbers of Ad–RM, Ad–LV–RM, LV–RM, and RV–RM marks, respectively, in the total catch. The resulting estimates of the 95 percent confidence intervals for the numbers of marked fish in the catch are: Ad–RM 21,616 ± 5.6 percent; Ad–LV–RM 4,285 ± 7.5 percent; Ad–RV–RM 2,141 ± 10.6 percent; LV–RM 174 ± 37.9 percent; RV–RM 266 ± 36.1 percent; where, for example, the 5.6 percent refers to the estimated number of Ad–RM marks (21,616) in the catch. Although these confidence interval estimates are approximate, they illustrate the general level of precision of the estimated total number of marks in the catch.

ESTIMATED CATCH OF 1961-BROOD HATCHERY FISH

In estimating the total number of marked hatchery fish in the catch on the basis of an observed number of mark recoveries and a sampling ratio, as was done in the preceding section, we made certain assumptions. These are assumptions 1, 2, and 3, which dealt with the permanence of fin marks, origin of observed fish marked with the hatchery marks, and accuracy of age assignments. Data presented in the preceding section supported these assumptions.

Additional assumptions are inherent in the procedure for estimating the catch of unmarked and, hence, total catch of hatchery fish. These are assumptions 4, 5, and 6, which were listed previously.

From the distribution of mark recoveries it appears that chinook salmon from Kalama and Spring Creek Hatcheries had different ocean distributions. It is not likely, then, that the first part of assumption 6 (same ocean distribution of fish from each hatchery) is satisfied. This poses no problem, however, provided the second part of assumption 6 (same proportion of fish marked at each hatchery) is satisfied. In this regard, it appears from appendix table 1 that with the possible exception of Klickitat Hatchery, proportions of Ad–RM marked fish in the releases were much the same at all of the hatcheries. Accordingly, we consider that assumption 6 is reasonably satisfied.

Information to test the assumption (assumption 5) concerning the distributions of marked and unmarked hatchery fish is limited. The distribution of marked fish is available from the present study; however, concurrent data for unmarked fish are lacking. The only information available on this subject is from a review by Cleaver (1967) of past tagging experiments in the ocean. Of 290 tagged fish recovered in the Columbia River from these experiments (during 1925–52 in coastal areas from northern Oregon to Cape Fairweather, Alaska), only 13 were recovered in hatcheries. Twelve of the 13 recoveries, however, had been tagged in areas off the west coast of Vancouver Island, Canada—an area of high concentration of marked hatchery fish as shown by recoveries of the marked 1961 brood. Although this result is consistent with assumption 5, it does not, of course, conclusively support it. The assumption must, therefore, remain an assumption.

The validity of assumption 4 (equality of maturity schedules and survival rates between marked (Ad–RM) and unmarked hatchery fish) can be examined by comparing the ratios of marked to unmarked fish at times of release and return. The marked to unmarked ratios by type of mark and age of fish for the 1961-brood hatchery returns are given in table 14. Ratios for Elokomin (LV–RM) and Oxbow (RV–RM) hatcheries are not presented because the number of recoveries was small.

TABLE 14.—*Marked to unmarked ratios for hatchery returns of 1961–brood chinook salmon by type of mark and age of fish*

Mark	Origin	Age (years)				
		2	3	4	5	All ages
		Marked/unmarked				
Ad–RM	All study hatcheries	0.059	0.063	0.075	0.106	0.067
Ad–RV–RM	Kalama	0	.016	.046	.092	.047
Ad–LV–RM	Spring Creek	.046	.038	.050	.062	.041
Ad–RM	Selected hatcheries [1]	.065	.067	.085	.081	.072

[1] Cascade, Oxbow, Little White Salmon, and Spring Creek Hatcheries.

The increase in ratios with age seems to indicate that marking had some delaying effect on the age of maturity. This effect was much greater for fish marked at Kalama than for fish marked at Spring Creek, although a similar type of mark was used. From the standpoint of survival, the ratios for all ages combined are smaller than those at release (table 4), thus indicating lower total survival for marked fish. The survival of Ad–RM marked fish, for example, was (0.067/0.1193)100=56.2 percent of that for the unmarked fish.

If the differences between the ratios of marked and unmarked fish at times of release and return are interpreted as indicative of delayed maturity or lower survival of marked fish, it is necessary to assume that all unmarked fish returning to a hatchery originated from that hatchery. It is apparent that straying [5] (provided the probability of straying is the same for marked and unmarked hatchery fish) reduces the marked to unmarked ratio for any given year of return. Thus, the indicated survival of marked fish relative to the survival of unmarked fish is too small. Also, if the probability that nonhatchery fish stray into a hatchery changes each year or is related to the age of fish, then the dilution of unmarked hatchery fish by nonhatchery fish in the return is disproportionate from year to year and the change in the marked to unmarked ratios with age of return is impossible to interpret.

Some of the hatcheries, such as Kalama Hatchery, are located on streams in which natural spawning occurs. In these cases, fish which are spawned at the hatcheries and comprise what we term "hatchery returns" are simply a selected sample (of various sizes in proportion to the total return) of adults returning to the stream. Marked to unmarked ratios would, therefore, be difficult to interpret in terms of the effects of marking on survival and age of maturity.

Only 5 of the 12 hatcheries (Bonneville, Cascade, Oxbow, Little White Salmon, and Spring Creek) are on streams that do not support natural spawning populations. Marked (Ad–RM) to unmarked ratios in the returns to four of these hatcheries, Bonneville Hatchery excluded,[6] are presented in table 14. The change in the ratio of marked to unmarked fish with age is not as pronounced as for the 12 hatcheries combined. In addition, the ratio, 0.072, for all ages is somewhat larger than it was for all 12 hatcheries, indicating that survival of marked (Ad–RM) fish relative to unmarked fish was (0.072/0.1193)100=60.4 percent.

Even for the four selected hatcheries, however, straying of nonhatchery fish into hatcheries is a possible source of error. Unfortunately, a direct measure of the extent of this straying is not available. General indications of straying of nonhatchery fish are obtained from observations of marked fish straying away from the hatcheries. Recoveries of specially marked fish released at Elokomin, Kalama, Oxbow, and Spring Creek Hatcheries are presented in table 15. Of the recoveries of marked fish at hatcheries and on spawning grounds, 71.4, 6.3, 38.0, and 4.9 percent of Elokomin, Kalama, Oxbow, and Spring Creek fish were recovered at places other than the release site. The higher percentage of strays from Elokomin and Oxbow Hatcheries may possibly be explained by the fact that 75 percent of the fish released at Elokomin and 30 percent of the fish released at Oxbow were the progeny of fish spawned at Spring Creek Hatchery.

Some indication that younger fish stray more than older fish can be seen in table 15. Groves, Collins, and Trefethen (1968) tagged two groups of chinook salmon at Spring Creek Hatchery and released them into the main stem of the Columbia

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[5] The term "straying" is used here in the sense that fish spawn or are spawned at a location other than their point of origin as fingerlings. Indeed, straying into a hatchery may be different from straying into a natural spawning area where the fish are free to leave again.

[6] Bonneville Hatchery is excluded because it is immediately below Bonneville Dam. The potential for straying may be greater if the fish are delayed in their upriver passage at the dam.

TABLE 15.—*Escapement recoveries of marked chinook salmon of 1961 brood by location of release and recovery and age of capture, 1963–66*

Recovery location [2]	Release location [1]															
	Elokomin				Kalama				Oxbow				Spring Creek			
	Age				Age				Age				Age			
	2	3	4	5	2	3	4	5	2	3	4	5	2	3	4	5
	Number of fish															
Grays River																
Big Creek			2													
Plympton		5														
Elokomin	2	2	0	0												
Abernathy																
Toutle																
Kalama						7	171	45								1
Lewis River (Speelyai)						5		4								
Washougal																
Tanner Creek (Bonneville)		1	1				4		1	12	5		1	1	1	
Eagle Creek (Cascade)										2			2	9		
Herman Creek (Oxbow)									1	35	12	1	1	6	2	
Wind River																
Little White Salmon									2	3	4					
Spring Creek		1				1	1				1		42	398	141	2
Big White Salmon														2		
Klickitat															4	
Total	2	9	3	0	0	13	176	49	4	52	22	1	46	416	148	3
Number of strays	0	7	3	0	0	6	5	4	3	17	10	0	4	18	7	1
Percentage strays	0	77.8	100.0	0	0	46.2	2.8	8.2	75.0	32.7	54.4	0	8.7	4.3	4.7	33.3
Percentage strays (all ages)	71.4				6.3				38.0				4.9			

[1] Elokomin: LV–RM; Kalama: Ad–RV–RM and Ad–RV; Oxbow: RV–RM; Spring Creek: Ad–LV–RM and Ad–LV.

[2] Recoveries in tributary streams were adjusted on the basis of the appropriate sampling ratios. Recovery locations are arranged in upstream order (see fig. 1).

River. A smaller fraction of the fish under 80 cm. (31.5 inches) long returned to Spring Creek than did the group over 80 cm. long (3-year-old chinook at Spring Creek average about 80 cm.).

These results offer an alternative explanation for the observed increase in the marked to unmarked ratio with age of return. That is, if the probability of straying is greater for younger fish than for older fish, as indicated above, then it is likely that the marked to unmarked ratio would increase with age even if marking had no effect on maturation.

Additional information of the effect of marking on maturation will be available later from the TM 50 marking experiment at Little White Salmon Hatchery. For the present, we will assume that marked and unmarked 1961-brood hatchery fish had the same maturity schedule.

Another point of interest in table 15 is that the fish generally strayed to areas near the hatchery of origin. Except for the one marked fish from Spring Creek recovered in the Kalama system all marked fish recovered at any great distance from the hatchery of origin were recovered upstream. If the pattern of straying is the same for nonhatchery fish, it is possible to obtain a maximum estimate of straying of nonhatchery fish into the four selected hatcheries—Cascade, Oxbow, Little White Salmon, and Spring Creek. These hatcheries are between Bonneville and The Dalles Dams (fig. 1). Most of the fall chinook salmon return to these hatcheries during the last week of August and September. Spawning occurs between mid-September and mid-October but is generally concentrated within a 2-week period.

Most (about 70 percent in 1965) of the fall chinook salmon that passed The Dalles Dam between August 26 and September 30 are generally brightly colored and are thought to spawn as much as a month later than the darker hatchery fish.[7, 8]

Because of the short duration of spawning at the four hatcheries, it is not likely that fish destined for areas above The Dalles Dam would contribute substantially to these hatchery returns. This generally agrees with the indicated "upstream" straying of the marked hatchery fish. That is, straying probably comes primarily from populations of fish that normally spawn near or downstream from the four hatcheries.

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[7] Smith, Eugene M. 1966. Final report. A study to identify the race of fall chinook salmon whose spawning grounds will be inundated by the John Day impoundment on the Columbia River. Fish Comm. Oreg. Res. Div. (U.S. Army Corps Eng., Walla Walla Dist., contract DA–45–164–CIVENG–66–5), 53 pp. [Processed.]

[8] McKee, Thomas B. 1966. Deschutes River adult fall chinook holding study, 1965. Fish Comm. Oreg. Res. Div. (U.S. Army Corps Eng., Walla Walla Dist., contract DA–45–164–CIVENG–66–7), 26 pp. [Processed.]

The difference between fall chinook salmon counts[9] at Bonneville and The Dalles Dams is an estimate of the number of fish removed by the fishery and spawning (aside from mortalities and passage through navigation locks where they are not counted) between the two dams.[10]

By subtracting the number of returns to the four selected hatcheries and the number removed by the fishery from this estimate, we obtain a maximum estimate of the fish that spawned between the two dams at sites other than the four hatcheries—these are the fish that did not stray into the four selected hatcheries. The estimate is maximum because it includes losses between the two dams and fish that strayed from the four hatcheries. Finally, by applying age composition data and estimates of straying (from observed straying of fish marked at Spring Creek Hatchery, table 15), we obtain estimates of the number of 1961-brood nonhatchery fish spawned at the four selected hatcheries (table 16).

An example of the information in table 16 follows. In 1963 an estimated 11,759 fall chinook salmon spawned between the two dams but not at the four subject hatcheries. An estimated 14 percent, or 1,646, were 1961-brood fish. We assumed that these fish are the (100−8.7)=91.3 percent of the nonhatchery fish that did not stray into the four hatcheries. The 8.7 was the observed percentage of the 2-year-old fish straying from Spring Creek Hatchery (table 15). It follows that (1,646/0.913)—1,646=157 nonhatchery fish strayed into the hatcheries. Similar calculations for 1964, 1965, and 1966 give an estimated total of 2,126 nonhatchery fish of the 1961 brood that were spawned at the four selected hatcheries during the 4 years.

Total return of marked (Ad–RM and Ad-only) and unmarked fish to the four hatcheries was 1,898 and 26,538 fish, respectively (appendix table 5). Subtracting the estimated number of nonhatchery strays, 2,126, from the unmarked return, we found the marked to unmarked ratio becomes 1,898/24,412=.078. Estimated survival of marked relative to the unmarked fish is then (.078/.1193) 100=65.4 percent.

TABLE 16.—*Estimated number of nonhatchery chinook salmon of 1961 brood spawned at four hatcheries [1] between Bonneville and The Dalles Dams, 1963–66*

Item	Year of run				Total
	1963	1964	1965	1966	
Count at Bonneville Dam [2]	121, 184	154, 534	134, 469	135, 095	545, 282
Count at The Dalles Dam [2]	66, 473	56, 150	87, 096	69, 018	278, 737
Hatchery returns [1]	24, 377	28, 409	12, 025	31, 023	95, 834
Catch [3]	18, 575	23, 338	25, 051	7, 008	73, 972
Bonneville count minus The Dalles count minus hatchery return minus catch	11, 759	46, 637	10, 297	28, 046	96, 739
Percent 1961 brood [4]	14	78	66	9	------
Number of 1961 brood year not straying	1, 646	36, 377	6, 796	2, 524	47, 343
Percent straying [5]	8. 7	4. 3	4. 7	0	--------
Estimated number of 1961-brood fish straying into four hatcheries [1]	157	1, 634	335	0	2, 126

[1] Spring Creek, Little White Salmon, Oxbow, and Cascade Hatcheries.
[2] Counts for period August 26 to September 30.
[3] Chinook catch between Bonneville and The Dalles Dams for period August 26 to September 30. Sport catch not included.
[4] Estimated age composition from fishery samples.
[5] Estimates from Spring Creek mark (Ad–LV–RM), table 11. Assumed 0 for age 5 because of the small number of returns.

This procedure for estimating the number of nonhatchery fish entering the hatcheries is subject to error. If, for example, the percentage straying was as large as 10 percent (for each age group), then the estimated total of 1961-brood nonhatchery fish that entered the four hatcheries would be 5,260; the estimate of the survival of marked to unmarked fish would then be 74.6 percent. In spite of the inexactness, however, it seems clear that the small value of the marked to unmarked ratio observed in the hatchery returns relative to that in the hatchery releases cannot be solely attributed to straying of nonhatchery fish. Furthermore, it appears that the total survival of marked (Ad–RM) relative to unmarked 1961-brood-year fish could not have exceeded 70 percent.

In summary, it appears from the present data that assumption 6 (equality of proportions marked at each hatchery) is satisfied, but for the present we must assume that marked and unmarked hatchery fish have the same ocean distribution and maturity schedules. In addition, we will assume that total survival of marked fish was 70 percent of the survival of unmarked fish—and further, that all additional mortality of marked fish occurred during their first year of life.

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[9] U.S. Army, Corps of Engineers. 1963-66. Annual fish passage report; North Pacific Division, Bonneville, The Dalles, McNary and Ice Harbor Dams, Columbia and Snake Rivers, Oregon and Washington, 1963–66. U.S. Army Eng. Dist., Corps Eng., Portland (Oreg.) and Walla Walla (Wash.). Various pagination.

[10] In an analysis of fishway counts (1957–65) at Bonneville and The Dalles Dams (among others), Fredd[11] found that the differences in counts of fall chinook salmon generally exceeded estimates of the numbers removed by the fishery and the numbers spawned in intermediate areas. He concluded that counting errors could not be a major contributor to the discrepancy, thus indicating a "loss" of fish between the two dams.

[11] Fredd, Louis C. 1966. Analysis of differences in fish counts at Columbia River dams, 1957–65. Fish Comm. Oreg. (U.S. Army Corps Eng. Portland Dist., contract DA–35–026–CIVENG–65 44), 47 pp. [Processed.]

On the basis of the preceding summary, estimates of the total catch of 1961–brood hatchery fish were made and are presented in table 17. These estimates were obtained from equation (6) and the estimated numbers of marked fish in the catch (table 10). For example, estimated 1964 total catch of hatchery fish (115,755) by the ocean commercial fisheries was computed as follows. First, the marked to unmarked ratio required in equation (6) was estimated by the product of the marked (Ad–RM) to unmarked ratio, 0.1193, at release (table 4) and the assumed relative survival of marked fish, 0.70. The catch of unmarked hatchery fish (104,227) was then estimated from the ratio: $104{,}227=8{,}704/(0.1193)(0.7)$ where 8,704 is the estimated catch of Ad–RM marked fish (including Ad-only). Estimated catches of the other marked hatchery fish were 2,031, 618, 89, and 86 for the Ad–LV–RM, Ad–RV–RM, LV–RM, and RV–RM marks, respectively.[12] The total catch of hatchery fish in 1964 is then simply the sum of the catches of marked and unmarked fish (i.e., $115{,}755=104{,}227+8{,}704+2{,}031+618+89+86$).

TABLE 17.—*Estimated catch of hatchery fall chinook salmon of 1961 brood by type of fishery and year of capture, 1963–66*

Fishery type	Year of catch				
	1963	1964	1965	1966	Total
	Number of fish				
Ocean sport	7, 597	27, 487	7, 514	1, 082	43, 680
Ocean commercial	43	115, 755	37, 441	4, 797	158, 036
Columbia River sport	0	272	33	0	305
Columbia River commercial	1, 942	32, 349	48, 275	2, 739	85, 305
Total	9, 582	175, 863	93, 263	8, 618	287, 326

During the 4 years of sampling an estimated 287,326 fall chinook salmon that originated from the 12 hatcheries were caught. This number comprised about 10 percent of the total catch (2,812,949) of 1961-brood chinook salmon in the fisheries sampled. The fish from these hatcheries accounted for 23, 11, 9, and 4 percent of the catches of 1961-brood chinook salmon in 1963, 1964, 1965, and 1966, respectively.

An approximate interval estimate [13] (95 percent confidence interval) for the total catch of hatchery fish is 258,593 to 316,059 (287,326±10 percent). This estimate is rough and is presented solely to indicate the general level of precision of the estimated catch of hatchery fish (287,326) obtained under the assumptions stated previously. Sources of error other than sampling variation are in fact more important at this time. For example, if survival of marked relative to unmarked fish was 60 or 100 percent, rather than the assumed 70 percent, then the estimated catch of hatchery fish would have been 330,465 or 209,672, respectively. Both of these values are well outside the interval estimate. It should, therefore, be clearly understood that the above estimated catch of hatchery fish (287,326), although reasonable (but probably minimal), is preliminary.

ESTIMATED VALUE OF CATCH FOR 1961–BROOD HATCHERY FISH

To determine the benefit to cost ratio of the 1961-brood-year releases of fall chinook salmon from the 12 hatcheries under study, estimates were made of production cost for the 53.6 million fish released and of the net value of the 287,326 fish caught by the sport and commercial fisheries. In addition to the release of 53.6 million fish from the 12 hatcheries, 3.86 million fish were released from Abernathy, Speelyai, Toutle, Klaskanine, and Sandy Hatcheries. By making certain assumptions it is also possible to estimate the catch and value of these releases.

The cost of producing fish released from the 12 hatcheries was estimated from 1962 fiscal year costs at individual hatcheries. Costs were apportioned between the brood year species groups at each hatchery on the basis of either estimated relative man-hours expended or relative size of each group. At each hatchery costs were divided into three categories:

1. Amortized and discounted capital investment
2. Fish food and drugs
3. Operational costs other than food

Capital investment in the hatcheries was amortized over 50 years and was charged a simple interest rate of 5 percent per annum,[14] which amounts to 7 percent of the total capital investment chargeable to each year's operation. This 7 percent was then apportioned among the broods and species present by using the percentage of time spent caring for each group of fish. Cost of fish food and drugs during the fiscal year was apportioned according to the pounds of each brood year-species group produced.[15] Operational cost other than food and drugs was apportioned the same as capital investment. This category includes personal services, travel, transportation of items, communication services, rents and utilities, other contractual services, equipment, supplies and materials, and administration.

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[12] Total estimates for LV–RM and RV–RM marks do not include the corresponding partial marks.

[13] Calculated by assuming that the variance of the estimate of the marked to unmarked ratio, $(.1193)(0.7)=0.0835$, in the catch is such that 2 times the standard deviation is equal to 0.0835.

[14] Amortization period and discount rate are from J. A. Crutchfield, Department of Economics, University of Washington, Seattle, Wash. (personal communication).

Klickitat Hatchery is used as an example of the above procedure. Table 18 shows the estimated cost ($68,773) to produce the 1961-brood fall chinook salmon at Klickitat Hatchery.

TABLE 18.—*Costs in rearing salmon at Klickitat Hatchery for fiscal year 1962, by brood and species*

Brood and species	Authorized and discounted capital investment	Fish food and related items	Operational costs other than food	Total
1961 fall chinook	$23, 169. 30	$4, 959. 82	$40, 643. 85	$68, 772. 97
1960 coho	6, 360. 20	4, 046. 17	11, 157. 14	21, 563. 51
1961 coho	12, 266. 10	2, 871. 48	21, 517. 33	36, 654. 91
1960 spring chinook	908. 60	130. 52	1, 593. 88	2, 633. 00
1961 spring chinook	2, 725. 80	1, 044. 17	4, 781. 63	8, 551. 60
Total	45, 430. 00	13, 052. 16	79, 693. 83	138, 175. 99

Capital investment through 1962 fiscal year for Klickitat Hatchery was $649,000. Seven percent, or $45,430, of this total, was attributable to the 1962 fiscal year. Because an estimated 51 percent of the man-hours was expended in caring for fall chinook salmon during fiscal year 1962, $23,169.30 (0.51 x 45,430) was the portion of the capital investment cost assigned to the fall chinook.

Total cost for food and drugs during the year at Klickitat Hatchery was $13,052.16. As 38 percent of the total weight of fish produced was fall chinook salmon, an estimated $4,959.82 (.38 x 13,052.16) of the food cost was assigned to them.

Total operational costs (other than food) were apportioned in the same manner as the capital investment. Hence, 51 percent or $40,643.85 of the year's operational cost ($79,693.83) was assigned to fall chinook salmon.

Adding these costs gives $68,772.97 as the estimated total cost in rearing the 1961-brood chinook salmon at Klickitat Hatchery. Following this procedure at each hatchery, we estimated the total cost in rearing the 1961-brood chinook salmon released at all hatcheries under study at $831,522.

To determine the benefit provided by the contribution of these hatchery releases to the commercial and sport fisheries, it is necessary to estimate their net economic value.

For commercially caught fish, the gross economic value was determined from estimated landings and average prices paid to fishermen in 1963–66. The standard benefit-cost technique would require the deduction of all associated costs, but on the basis of arguments similar to those presented by Crutchfield, Kral, and Phinney,[16] we assumed that the capacity of present commercial salmon fisheries in terms of vessels and gear is such that additional catches can be made with little increase in cost.

The above assumption is supported in part from an examination of recent catch and effort data for the Washington and British Columbia troll fisheries (table 19). The two fisheries accounted for over 90 percent of the estimated ocean commercial catch of hatchery fish. Beginning in 1958, the size (number of boats) of the troll fleet increased considerably. The increase was not accompanied, however, by a corresponding increase in the catch of chinook and coho salmon (target species of the troll fisheries). The average catch per boat for 1958–62 was 390–40 percent less than the average catch per boat of 650 for the preceding period (1952–57). Even with the increased catches during 1963–66, the average catch per boat (assuming the number of boats was at least as great as during 1958–62) was only about 550—again, considerably less than the 1952–57 level. It seems reasonably clear from these data that the catch capacity of the troll fleet of Washington and British Columbia is greater than their present success. Larger catches could, therefore, be made without investment in additional units of gear.

The assumption (excess fishing capacity) is also indicated for the Columbia River gill-net fishery, which together with the above two troll fisheries accounted for over 95 percent of the estimated com-

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[15] Amount of food given to the various groups of fish at a hatchery is generally proportional to their weight.

[16] Crutchfield, James A., Kenneth B. Kral, and Lloyd A. Phinney. 1965. An economic evaluation of Washington State Department of Fisheries controlled natural-rearing program for coho salmon (*Oncorhynchus kisutch*). Wash. Dep. Fish., Res. Div. (U.S. Fish Wildl. Serv. contract #14-17-0007-246, Part II), 26 pp. [Processed.]

Table 19.—*Catch of chinook and coho salmon and number of boats in commercial troll fisheries of Washington and British Columbia, 1952–66*

Year	Catch of fish [1]	Boats [2]
	Millions	*Number*
1952	4.09	5979
1953	3.48	5410
1954	2.75	5240
1955	3.03	4560
1956	3.15	4277
1957	3.34	5061
1958	3.32	6606
1959	2.64	7511
1960	1.86	7390
1961	2.91	7654
1962	3.16	7115
1963	3.11	
1964	3.79	
1965	4.26	
1966	4.77	

[1] Washington State Department of Fisheries (1964) and International North Pacific Fisheries Commission (1952–66).

[2] Cleaver (1967): data are actually number of licenses sold.

mercial catch of hatchery chinook salmon of the 1961 brood. To conserve the chinook salmon resource, fishing seasons have been steadily shortened (Pulford, 1964). The length of the fishing season has been decreased from 272 days in 1936 to 101 days in 1960 and 80 days in 1966. It would seem, then, that the present fishery is capable of making additional catches without increasing the present number of fishing units.

We also assume that additional running expenses of vessels and labor costs—attributed to the contribution of these hatcheries to the salmon resource—are negligible for the present fisheries. This assumption is reasonable if one considers: (1) the estimated catch of hatchery fish (287,000 fish) is small compared to annual catches of salmon (e.g., Washington and British Columbia troll catches, table 19), and (2) crews of vessels engaged in fishing are effectively precluded from working at other occupations during closed fishing periods (Crutchfield et al.).[16]

Thus, the gross economic value to the commercial fisherman of additional catches of chinook salmon made possible by hatchery releases essentially constitutes a net benefit.

Estimation of net value for the catch of hatchery chinook salmon by sport fishermen was made from an assumed net value per fish of \$8.87.[17] This value represents an estimate of the amount an angler is willing to pay for the right to fish. It was obtained by extrapolation from a 1962 survey of Oregon salmon-steelhead anglers reported upon by Brown, Singh, and Castle (1964).

Calculation of total net value (\$1,917,003) of the commercial and sport catch of fall chinook salmon that originated from the hatcheries under study is shown in table 20. The benefit to cost ratio is obtained from the ratio \$1,917,003/\$831,522 and is estimated as 2.3 : 1.

This benefit to cost ratio applies, of course, only to chinook salmon at the study hatcheries. As indicated above for Klickitat Hatchery (table 18), other species of salmon (principally coho) are raised at these hatcheries. To fully use all production facilities, the hatchery complex is now managed on a multispecies basis. A more complete and meaningful benefit to cost analyses of the hatchery system must, therefore, await completion (1969) of the study of the contribution that hatchery-reared coho salmon make to the fisheries.

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[17] U.S. Department of the Interior, Bureau of Commercial Fisheries, Division of Economics. 1966. An economic evaluation of Columbia River anadromous fish programs. 58 pp. [Processed.]

Table 20.—*Estimated value of the catch of fall chinook salmon of 1961 brood that were released from study hatcheries, by type of fishery*

Fishery	Age	Fish	Sample size	Average weight [1]		Total weight [1]		Value per unit catch [2]	Total value
		Number	*Number of fish*	*Lbs.*	*Kg.*	*Lbs.*	*Kg.*	*Dollars*	*Dollars*
Sport	All	43,985						[3] 8.870	390,147
Ocean commercial	2	43	27	4.00	1.81	172	78	.380	65
	3	115,755	2,040	8.45	3.83	978,130	443,689	.435	425,487
	4	37,441	538	15.29	6.94	572,473	259,653	.610	349,208
	5	4,797	56	18.71	8.49	89,752	40,712	.650	58,339
Columbia River commercial	2	1,942	22	6.11	2.77	11,866	5,381	.360	4,272
	3	32,349	870	17.98	8.16	581,635	263,838	.360	209,389
	4	48,275	1,135	26.10	11.84	1,259,978	571,528	.360	453,592
	5	2,739	57	28.13	12.76	77,048	34,950	.344	26,504
Total		287,326							1,917.003

[1] Weights for ocean commercial fisheries are dressed weights, and those for Columbia River fisheries are round weights. Original weights were in pounds for Ad–RM marked fish.

[2] Entries for commercial fisheries (dollars per pound) are based on prices paid for Washington State troll landings obtained from Dale Ward, Washington State Department of Fisheries (personal communication).

[3] See footnote 17 of text.

It must further be understood that hatchery methods have changed significantly since 1962. This change is reflected in the increased size of fish released from hatcheries. For example, the average weight of fall chinook salmon released from Columbia River hatcheries operated by Washington Department of Fisheries increased from 2.18 g. in 1962 to 3.89 g. in 1966.[18] It is likely, therefore, that survival of hatchery fish and, hence, the contribution of given numbers released has changed since 1962.

To estimate the value of the catch of 1961-brood fall chinook salmon from all Columbia River hatcheries, we must assume that the 3.86 million fish released from hatcheries not included in the study contributed to the fisheries in the same proportion as the fish released (53.65 million) from the hatcheries under study. On this basis the value of the catch of these releases would be:

$$137{,}832 = \frac{(3.86)\ (1{,}917{,}003)}{(53.65)}$$

or about $138,000. The value of the catch of fish released from all hatcheries is then estimated as $2,055,000.

Because of the conservative nature of the estimate of survival of marked fish relative to unmarked fish, we believe that the estimated value of the catch of hatchery fish, as well as the benefit-cost estimate presented above, is minimal.

SUMMARY

1. During 4 years of marking at 12 hatcheries, 21.3 million fish (10 percent of the total production of 213 million) were marked with an adipose-maxillary mark. An additional 9.6 million were identified with special marks unique to a hatchery.

2. The 1961-brood release of 53.6 million fish included 5.4 million (10.1 percent of the total release) marked with a "common mark" (Ad–RM). Fish with marks unique to a hatchery were released from Elokomin, Kalama, Oxbow, and Spring Creek Hatcheries.

3. Auxiliary data collected suggested that the quality of marking and the permanence of marks (except possibly for the maxillary mark in the 1961 and 1962 broods) were reasonably satisfactory.

4. During the first 4 years of mark sampling (1963–66), an average of 23 percent of the chinook salmon catch was examined for marked fish.

5. Except for 1963, sampling for marked fish was conducted in most chinook fisheries from Monterey, Calif., northward to southeast Alaska. In 1963, sampling was limited to the Washington, Oregon, and Columbia River fisheries.

6. A total of 9,573 marked fish from the 1961 brood of possible Columbia River hatchery origin were recovered during the 4 years. The majority, 6,189, were recovered as age–3 fish in 1964.

7. Although marked fish were recovered in the ocean fisheries over the entire range of sampling, most were recovered from landings made north of the Columbia River mouth (Washington and west coast of Vancouver Island fisheries).

8. Marked fish that originated from Kalama Hatchery were the only ones (specific to a hatchery) recovered in the southeast Alaska fishery. In general, proportionately more of the Kalama fish were recovered in the northern parts of the sampling range than were the marked fish originating from Elokomin, Oxbow, or Spring Creek Hatcheries.

9. An estimated total of 21,600 marked (Ad–RM) fish that originated from the 12 study hatcheries were caught. An additional 3,400 escaped the fisheries and returned to spawn.

10. The estimated average catch to escapement ratio for the hatcheries under study was about 6:1. For marked fish from Elokomin, Kalama, Oxbow, and Spring Creek Hatcheries this ratio was 12:1, 9:1, 3:1, and 7:1, respectively.

11. The catch of Ad-RM marked fish from all 12 hatcheries in terms of the numbers released was 3.97 per 1,000 released. This quantity was 4.50 and 3.78 for Kalama and Spring Creek Hatcheries, respectively. The contribution per 1,000 released for Elokomin and Oxbow Hatcheries was at most only one-half that for Kalama and Spring Creek.

12. By assuming that marked and unmarked hatchery fish have the same ocean distribution and maturity schedules and that survival of marked fish was 70 percent of the survival of unmarked fish, we estimated that the total catch of hatchery fish (marked and unmarked) was 287,326.

13. The estimated catch, 287,326, of hatchery fish comprised about 10 percent of the total catch

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[18] Harry Senn, Washington State Department of Fisheries (personal communication).

of 1961-brood chinook salmon in the fisheries sampled.

14. If survival of marked relative to unmarked fish was 60 or 100 percent rather than the assumed 70 percent, then the estimated catch of hatchery fish would have been 330,465 or 209,672, respectively. The latter value is considered too low: it is not likely that the survival of marked fish exceeded 70 percent of the survival of unmarked fish.

15. The estimated cost of rearing the fall chinook salmon of the 1961 brood released from the study hatcheries was $831,522. The estimated net value to the fishermen of the catch of these fish was $1,917,003. The benefit to cost ratio was, therefore, 2.3 :1.

16. The estimated total value of the catch of fall chinook salmon of 1961 brood that originated from all Columbia River hatcheries (including five hatcheries not participating in the marking experiment) was $2,055,000.

17. We considered that the estimated catch of hatchery fish, and, therefore, the value and benefit-ratio, is minimum.

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Many agencies and individuals assisted us. The Canadian Government financed and conducted an excellent program of mark sampling in the British Columbia fisheries. Without such sampling we would have been seriously handicapped. The State fishery agencies provided research and management personnel and necessary catch data. Charles O. Junge, Jr., Fish Commission of Oregon, and Reynold A. Fredin, Bureau of Commercial Fisheries, developed the original design of the hatchery evaluation study. Harold Godfrey, Fisheries Research Board of Canada; Gary Finger, Alaska Department of Fish and Game; Emanuel A. LeMier, Richard E. Noble, and Harry Senn, Washington Department of Fisheries; Fred E. Locke, Oregon Game Commission; Ernest R. Jeffries, Earl F. Pulford, Roy E. Sams, and Robert E. Loeffel, Fish Commission of Oregon; Harlan E. Johnson, Roger Burrows, Robert Combs, Joseph Elliot, and Warner G. Taylor, Bureau of Sport Fisheries and Wildlife; Paul T. Jensen, California Fish and Game Department, and the many members of their respective agencies gave their time and effort. James A. Crutchfield reviewed the economic section.

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Appendix Table 1.—*Estimated numbers of fall chinook salmon fingerlings of 1961 brood released from Columbia River hatcheries*

Hatchery	Fish released		Proportion of fish marked				Fish marked			
			Proportion		Standard deviation		Total		Standard deviation	
	Total	Standard deviation	Ad-RM	Special mark	Ad-RM	Special mark	Ad-RM	Special mark	Ad-RM	Special mark
	Number	*Number*					*Number*	*Number*	*Number*	*Number*
Grays River	893, 028	20, 240	0. 0951		0. 00310		84, 927		3, 370	
Elokomin	1, 575, 000	33, 888	. 0937	(LV-RM) 0. 3051	. 00232	0. 00366	147, 578	480, 533	4, 837	11, 838
Kalama	4, 906, 845	65, 737	. 1013	(Ad-RV-RM) . 0970	. 00136	. 00133	497, 063	475, 964	9, 364	9, 165
Washougal	2, 314, 940	46. 983	. 0932		. 00191		215, 752		6, 219	
Little White Salmon	12, 077, 844	348, 596	. 1061		. 00280		1, 281, 459		50, 338	
Spring Creek	10, 925, 933	229, 319	. 1033	(Ad-LV-RM) . 1037	. 00203	. 00203	1, 128, 649	1, 133, 019	32, 409	32, 659
Big White Salmon	3, 545, 865	133, 488	. 0947		. 00348		335, 793		17, 655	
Klickitat	3, 177, 958	133, 217	. 0891		. 00508		283, 153		20, 075	
Oxbow	4, 549, 959	76, 956	. 1034	(RV-RM) . 0990	. 00137	. 00134	470, 466	450, 446	10, 100	9, 762
Cascade	4, 842, 554	81, 014	. 1015		. 00132		491, 519		10, 401	
Bonneville	3, 829, 617	71, 368	. 1054		. 00150		403, 642		9, 472	
Big Creek	1, 013, 671	26, 210	. 1050		. 00292		106, 435		4, 039	
Total	53, 653, 214	568, 071	. 1015		. 00088		5, 446, 439		74, 630	

Appendix Table 2.—*Estimated numbers of fall chinook salmon fingerlings of 1962 brood released from Columbia River hatcheries*

Hatchery	Fish released		Proportion of fish marked				Fish marked			
			Proportion		Standard deviation		Total		Standard deviation	
	Total	Standard deviation	Ad-LM	Special mark	Ad-LM	Special mark	Ad-LM	Special mark	Ad-LM	Special mark
	Number	*Number*					*Number*	*Number*	*Number*	*Number*
Grays River	1, 359, 761	27, 825	0. 0936	(LV-LM) 0. 1776	0. 00249	0. 00327	127, 274	241, 494	4, 273	6, 648
Elokomin	*2, 391, 219	61, 000	. 0934		. 00195		223, 340		7, 360	
Kalama	4, 599, 326	102, 405	. 0938	(Ad-RV-LM) . 0952	. 00135	. 00136	431, 206	437, 669	11, 272	11, 632
Washougal	3, 315, 613	84, 648	. 0956		. 00161		316, 973		9, 687	
Little White Salmon	11, 588, 405	171, 575	. 1022		. 00088		1, 183, 865		20, 298	
Spring Creek	8, 408, 267	146, 575	. 1033	(Ad-LV-LM) . 1031	. 00105	. 00105	868, 574	866, 892	17, 521	17, 496
Big White Salmon	3, 438, 295	55, 505	. 0993		. 00160		341, 554		7, 818	
Klickitat	2, 624, 470	35, 540	. 0889		. 00170		233, 315		5, 479	
Oxbow	4, 916, 873	76, 396	. 0951		. 00127		467, 595		9, 576	
Cascade	4, 217, 910	66, 149	. 1021	(RV-LM) . 1283	. 00141	. 00156	430, 649	541, 158	9, 000	10, 735
Bonneville	4, 635, 279	73, 539	. 1139		. 00150		527, 958		10, 895	
Big Creek	974, 585	20, 996	. 0993		. 00290		96, 776		3, 513	
Willard **										
Total	52, 470, 003	366, 201	. 1000		. 00041		5, 249, 079		42, 532	

*Includes an estimated 169,000 fish not sampled at release. ** Included in the release for Little White Salmon.

APPENDIX TABLE 3.—*Estimated numbers of fall chinook salmon fingerlings of 1963 brood releasea from Columbia River hatcheries*

Hatchery	Fish released		Proportion of fish marked				Fish marked			
			Proportion		Standard deviation		Total		Standard deviation	
	Total	Standard deviation	Ad-RM	Special mark	Ad-RM	Special mark	Ad-RM	Special mark	Ad-RM	Special mark
	Number	*Number*					*Number*	*Number*	*Number*	*Number*
Grays River	1, 576, 680	20, 798	0. 1023		0. 00234		161, 294		4, 263	
Elokomin	2, 383, 919	31, 374	. 0912		. 00181		217, 413		5, 179	
Kalama	4, 883, 937	85, 028	. 0987	(Ad-RV-RM) 0. 0934	. 00133	0. 00130	482, 176	456, 158	10, 490	10, 119
Washougal	3, 157, 696	38, 786	. 0953		. 00160		300, 928		6, 268	
Little White Salmon	11, 915, 503	186, 493	. 0936		. 00084		1, 115, 614		20, 208	
Spring Creek	7, 467, 629	131, 916	. 1032	(Ad-LV-RM) . 1006	. 00111	. 00110	770, 659	751, 243	15, 934	15, 607
Big White Salmon	2, 448, 904	49, 017	. 0998		. 00191		244, 401		6, 768	
Klickitat	2, 888, 208	37, 171	. 0974	(LV-RM) . 1806	. 00169	. 00220	281, 311	521, 610	6, 086	9, 238
Oxbow	6, 124, 048	91, 818	. 1051		. 00119		643, 637		12, 083	
Cascade	5, 734, 238	75, 382	. 0991		. 00122		568, 091		10, 228	
Bonneville	9, 545, 463	141, 289	. 1059		. 00095		1, 010, 865		17, 515	
Big Creek	1, 985, 838	28, 781	. 0957	(RV-RM) . 2920	. 00208	. 00322	190, 075	579, 967	4, 987	10, 545
Total	60, 112, 063	356, 945	. 0996		. 00037		5, 986, 464		42, 071	

APPENDIX TABLE 4.—*Estimated numbers of fall chinook salmon fingerlings of 1964 brood released from Columbia River hatcheries*

Hatchery	Fish released		Proportion of fish marked				Fish marked			
			Proportion		Standard deviation		Total		Standard deviation	
	Total	Standard deviation	Ad-LM	Special mark	Ad-LM	Special mark	Ad-LM	Special mark	Ad-LM	Special mark
	Number	*Number*					*Number*	*Number*	*Number*	*Number*
Grays River	1, 369, 522	28, 017	0. 0938		0. 00248		128, 461		4, 300	
Elokomin	2, 069, 739	32, 740	. 0935		. 00204		193, 485		5, 199	
Kalama	3, 496, 560	67, 730	. 0993	(Ad-RV-LM) 0. 0914	. 00158	0. 00152	347, 248	319, 412	8, 691	8, 215
Washougal	2, 643, 924	50, 114	. 1004		. 00184		265, 450		7, 005	
Little White Salmon	8, 365, 579	120, 972	. 0995	(RV-LM) . 0953	. 00108	. 00105	832, 221	797, 345	14, 996	14, 530
Spring Creek	6, 554, 455	86, 840	. 1031	. 0917	. 00122	. 00116	675, 493	600, 953	11, 999	10, 921
Big White Salmon	2, 007, 409	32, 925	. 0874		. 00208		175, 448		5, 072	
Klickitat	2, 935, 065	54, 478	. 0934		. 00172		274, 135		7, 174	
Oxbow	1, 290, 497	17, 367	. 0949		. 00248		122, 516		3, 599	
Cascade	4, 709, 551	72, 825	. 1044		. 00134		491, 677		9, 896	
Bonneville	9, 887, 575	121, 640	. 1000	(LV-LM) . 0968	. 00093	. 00092	988, 974	957, 110	15, 242	14, 876
Big Creek	1, 448, 676	19, 111	. 0988		. 00241		143, 129		3, 964	
Total	46, 778, 552	258, 073	. 0992		. 00044		4, 638, 237		32, 729	

APPENDIX TABLE 5.—*Marked and unmarked returns of fall chinook salmon of 1961 brood year to Columbia River hatcheries and tributary streams*

Recovery location	Group	Year of return			
		1963	1964	1965	1966
		Number of fish			
Hatcheries:					
Grays River	Unmarked	0	35	34	0
	Ad-RM	0	0	1	0
Big Creek	Unmarked	103	902	281	6
	Ad-RM	5	33	20	0
	Ad	1	2	3	0
	LV	0	0	1	0
Elokomin	Unmarked	11	414	8	0
	Ad-RM	0	3	0	0
	Ad	0	1	0	0
	LV-RM	2	2	0	0
	LV	0	7	0	0
Kalama	Unmarked	49	434	2, 429	411
	Ad-RM	0	20	134	47
	Ad	0	2	2	0
	Ad-RV-RM	0	7	111	38
	Ad-LV-RM	0	0	0	1
Washougal	Unmarked	14	53	12	3
	Ad-RM	1	2	0	0
Bonneville	Unmarked	369	2, 527	1, 867	13
	Ad-RM	13	157	84	1
	Ad	0	14	36	0
	Ad-LV	1	1	1	0
	Ad-RV	0	0	4	0
	LV-RM	0	1	1	0
	LV	0	0	1	0
	RV-RM	1	12	5	0
	RV	1	0	4	0
Little White Salmon	Unmarked	197	3, 429	2, 035	45
	Ad-RM	9	158	139	1
	Ad	1	45	41	0
	LV	0	0	1	0
	RV-RM	2	3	4	0
	RV	1	0	1	0
Cascade	Unmarked	156	2, 010	1, 078	38
	Ad-RM	5	117	64	1
	Ad	2	1	13	0
	Ad-LV-RM	2	8	0	0
	Ad-LV	0	1	0	0
	RV-RM	0	2	0	0
Spring Creek	Unmarked	922	10, 374	2, 849	32
	Ad-RM	57	641	190	6
	Ad	17	130	64	2
	Ad-LV-RM	38	353	119	1
	Ad-LV	4	45	22	1
	Ad-RV-RM	0	1	1	0
	LV-RM	0	1	0	0
	LV	0	0	2	0
	RV-RM	0	0	1	0
	RV	0	1	0	0
Oxbow	Unmarked	242	2, 457	666	8
	Ad-RM	4	116	47	0
	Ad	3	16	8	0
	Ad-LV-RM	1	2	2	0
	Ad-LV	0	4	0	0
	LV	0	1	0	0
	RV-RM	1	35	12	1
	RV	1	6	5	0
Big White Salmon	Unmarked	17	1, 064	(*)	(*)
	Ad-RM	0	33	(*)	(*)
	Ad	0	4	(*)	(*)
	Ad-LV-RM	0	1	(*)	(*)
Klickitat	Unmarked	15	334	38	0
	Ad-RM	6	16	0	1
Toutle	Unmarked	(*)	956	1, 289	107
Abernathy	Unmarked	(*)	1, 797	661	0
	Ad-RM	(*)	1	0	0
	LV	(*)	2	2	0
Speelyai	Unmarked	(*)	1, 202	2, 084	0
	Ad-RM	(*)	4	0	0
	Ad-RV-RM	(*)	5	0	0
Tributary streams: [1]					
Big Creek	Unmarked	(*)	313	362	1
	Ad-RM	(*)	5	11	0
	Ad	(*)	0	2	0
	LV-RM	(*)	0	2	0
Kalama	Unmarked	(*)	6, 330	2, 884	120
	AD-RM	(*)	0	161	14
	Ad	(*)	45	7	0
	Ad-RV-RM	(*)	0	56	7
	Ad-RV	(*)	0	4	0
Little White Salmon	Unmarked	(*)	30	34	4
	Ad-RM	(*)	1	3	0
Big White Salmon	Unmarked	(*)	905	956	45
	Ad-RM	(*)	9	6	2
	Ad	(*)	1	0	0
	Ad-LV-RM	(*)	1	0	0
Klickitat	Unmarked	(*)	12, 496	3, 907	22
	Ad-RM	(*)	370	162	0
	Ad	(*)	22	0	0
	Ad-LV-RM	(*)	0	4	0
Plympton	Unmarked	(*)	333	172	1
	Ad-RM	(*)	8	4	0
	Ad	(*)	6	2	0
	LV-RM	(*)	5	0	0
Grays	Unmarked	(*)	87	36	0
	Ad-RM	(*)	0	2	0
Washougal	Unmarked	(*)	333	172	16
	Ad-RM	(*)	0	4	0
Wind	Unmarked	(*)	422	34	0
	Ad-RM	(*)	0	2	0
Lewis	Unmarked	(*)	643	160	1, 835
	Ad-RM	(*)	0	0	5
	Ad-RV-RM	(*)	0	0	2
	Ad-RV	(*)	0	0	2
	LV	(*)	0	0	2
Elokomin	Unmarked	(*)	(*)	421	0

See footnotes at end of table.

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*Not sampled

[1] Total return of marked fish for tributary stream estimated from mark recoveries.

EFFECTS OF PESTICIDES ON EMBRYONIC DEVELOPMENT OF CLAMS AND OYSTERS AND ON SURVIVAL AND GROWTH OF THE LARVAE

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ABSTRACT

Fifty-two compounds were tested for their effects on embryos of the hard clam, *Mercenaria mercenaria*, and the American oyster, *Crassostrea virginica*, and on their larvae. The pesticides included 17 insecticides, 12 herbicides, one nematocide, four solvents, and 18 miscellaneous bactericides, fungicides, and algicides.

Most of the compounds affected embryonic development more than survival or growth of larvae. Some, however, drastically reduced growth of larvae at concentrations that had relatively little effect on embryonic development. It is necessary, therefore, to evaluate the effects of pesticides on all stages of the life cycle of an organism before the pesticide can be considered safe. Nevertheless, differences in toxicity to bivalve larvae among compounds of each category of pesticide are large enough that it should be possible to select compounds to control pest species without serious damage to commercial shellfish.

The extensive use in recent years of highly persistent pesticides for control of certain insects and undesirable plants, not only on agricultural lands but also on recreational areas, lakes, streams, and marshes, has made imperative an evaluation of the effects of these compounds on fish and wildlife. The eventual goal is to control undesirable species, with the least harm to the desirable members of the ecosystem. Attainment of this goal requires extensive knowledge of how each pesticide affects each species or representative species of the system. Also, the pesticide must be highly specific or be applied so that its dispersion is strictly limited.

Pesticides may enter the habitat of shellfish in several ways. One is by being carried there in runoff water from treated land areas. Cottam (1960) stated that 2 to 3 billion pounds (9.07 to 13.61 x 10^8 kg.) of pesticides are used annually in the United States on about 100 million acres (40.5 x 10^6 ha.) of land. Thimann (1964) stated that the United States used 175,000 short tons (158,760 metric tons) of insecticides in 1962 and about half that much of fungicides and herbicides. Doudoroff, Katz, and Tarzwell (1953) made laboratory tests of soils collected from toxaphene-treated fields and concluded that stream waters can be made toxic to fish by the drainage from such fields. Such runoff water may carry the pesticides in solution, adsorbed on suspended particles, or incorporated in plants and animals in the water. Certainly, large quantities of the pesticides that leach from the soil must eventually reach coastal marine waters and sediments.

A second, more direct, and perhaps more easily regulated method by which pesticides may enter the estuarine environment is the use of insecticides and herbicides on salt marshes and estuaries to control mosquitoes and undesirable plants. In some regions large areas are sprayed near shellfish beds. Pesticides used in this way probably create higher concentrations of the active ingredients in the estuarine water than are achieved by any other method.

Loosanoff, MacKenzie, and Shearer (1959[2]), Loosanoff et al. (1960), and Loosanoff (1961) proposed the use of several pesticides for the control of certain predators and competitors of

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[2] Loosanoff, V. L., C. L. MacKenzie, Jr., and L. W. Shearer. 1959. Use of chemical barriers to protect shellfish beds from predators. Bur. Commer. Fish. Biol. Lab., Milford, Conn., Bull. 6, 23: 1-11.

commercial shellfish. The methods of application proposed by these authors, however, were designed to restrict the dispersal of the pesticide. Compounds relatively insoluble in water were dissolved in polychlorinated benzenes, which are themselves virtually insoluble in water—a characteristic that further limited the solubility of the pesticide. Moreover, the polychlorinated benzenes, which are heavier than sea water, were mixed with dry sand to anchor the pesticide to the bottom of the particular shellfish bed treated. This essentially two-dimensional treatment of limited areas with a control pesticide had little or no effect on pelagic or planktonic organisms.

Butler, Wilson, and Rick (1962) presented data on the effects of some pesticides on adult oysters and Davis (1960) reported the effects of 31 compounds, including several types of pesticides, on fertilized eggs and larvae of bivalves. The authors of the two papers considered the effect of pesticides on growth to be the most sensitive index for these mollusks.

The highest concentration of any pesticide that can be considered "safe" for use in waters in which valuable species of bivalves reproduce is the highest concentration that has no appreciable effect on survival of the developing embryo or on growth and survival of the fully formed veliger larvae. It is also necessary to determine the concentrations tolerated by spawning individuals and by organisms that serve as food for larval and adult bivalves (Ukeles, 1962).

A distinction is made between effects on development of the embryo and on survival and growth during the larval stage because tolerances of these two pelagic stages to a given toxicant are often markedly different. Growth of the veliger larvae, moreover, may be drastically retarded at concentrations of toxicants too low to cause direct mortality of either embryonic or larval stages. Such a retardation of growth, however, serves to prolong the pelagic life of the larvae and, thus, increases the chance for their loss through predation, disease, and dispersion.

This report summarizes the data obtained at the Bureau of Commercial Fisheries Biological Laboratory in Milford concerning the effects of various compounds used in control of various types of undesirable organisms, on the development of fertilized eggs of hard clams, *Mercenaria mercenaria*, and American oysters, *Crassostrea virginica*, and on the survival and growth of the larvae. The data, unfortunately, are not complete for all of the compounds tested. The work on pesticides at the laboratory in Milford has been terminated by transfer of pesticide work to the Bureau's Biological Laboratory at Gulf Breeze, Fla. In the early experiments the effects of the compounds on development of fertilized eggs were not determined and many were tested in only a single experiment. Furthermore, for some experiments in which growth of larvae in control cultures was not satisfactory, we can give only the data on development of fertilized eggs. The effects of a number of these pesticides on some of the algal foods of bivalve larvae have also been determined (Ukeles, 1962).

METHODS

Methods for spawning oysters out of season and standard methods for culturing the larvae have been described in detail by Loosanoff and Davis (1963). These methods were followed throughout the present series of experiments.

In most experiments all pesticides were tested at concentrations of 0.25, 0.50, 1, 2.5, 5, and 10 p.p.m. (parts per million), with duplicate cultures at each concentration. If a toxic range was not established in the first experiment, these concentrations were increased or decreased by a factor of 10 in the next experiment. Usually, however, the range of 0.25 to 10 p.p.m. included concentrations that had no effect and concentrations that caused 100 percent mortality. Stock solutions of water-soluble pesticides were made up in water; all others were made up in acetone, except for a very few that were insoluble in either water or acetone. The latter were used as water suspensions.

For observations on development of embryos, fertilized eggs were introduced into the test concentrations soon after release and fertilization, usually when the eggs were in the two-cell stage of development. Quantitative samples were taken 48 hours later to determine the percentage of the fertilized eggs in each culture that had developed to normal straight-hinge veliger larvae.

For tests to determine the effect of compounds on survival and growth of veliger larvae, we used cultures of 2-day-old larvae that had been reared to the straight-hinge stage under normal conditions. These larvae were then reared, in the different concentrations of substances being tested, for a period of 10 days for clam larvae or 12 days for oyster larvae. Thus, when the quantitative samples were taken at the end of the period, the larvae were 12 and 14 days old, respectively. These periods represent the normal time of setting for the two species under good environmental conditions at the temperatures used (24° ± 1° C.).

We fed the test larvae a mixture of live flagellates, generally at a rate of 0.01 ml. of packed cells to each 1-liter culture per day. Sea water and test compound were renewed in the cultures every second day. The contents of a culture vessel were washed onto a stainless steel screen that retained the larvae but allowed the sea water and dissolved pesticide to pass through. The Pyrex[3] culture vessels used in the experiments were then thoroughly washed before the larvae and the fresh solution of pesticide in sea water were again added. The renewal of the culture medium every second day in this manner minimized the buildup of harmful metabolites and made it possible to maintain accurately the concentration of test compound at the desired level.

Quantitative samples, consisting of 1.6 percent of the total larval population of a culture, were taken at the end of the 2-day and the 12- or 14-day experimental periods and preserved for microscopic examination. We determined the survival by counting the number of larvae that had been living at the time of preservation. Survival values (table 1, cols. 1, 2) are expressed as a percentage (R) of the survival in control cultures and were calculated as follows:

$$R=\frac{\text{Average number of larvae in experimental cultures}}{\text{Average number of larvae in control cultures}}\times 100$$

Growth, or increase in mean lengths in the 12- and 14-day experiments (table 1, col. 3), is expressed as a percentage (G) of the increase in mean length of larvae in control cultures and was calculated as follows:

$$G=\frac{\text{Mean length of larvae in experimental cultures}-\text{mean length at 2 days}}{\text{Mean length of larvae in control cultures}-\text{mean length at 2 days}}\times 100$$

Mean length was determined by measuring the maximum length of the shell, parallel to the hinge line, of 100-oyster larvae or of 50-clam larvae from the preserved samples. The expression of results as percentages of the increase in mean length and survival of larvae in control cultures made possible the direct comparison of data from the different experiments.

Measurements of effects of toxicants on growth and survival of larvae are subject to considerable error due to random sampling error and variations introduced by the slight uncontrolled environmental differences between cultures. In addition, changes in sea water and food quality between successive experiments undoubtedly caused variation in observed effects. These factors must be taken into consideration in judging reliability of the data and in ascertaining safe and harmful levels of the test compound.

The standard error in measurements of growth is considerably greater for oyster larvae than for clam larvae. A length-frequency distribution of clam larvae receiving a given treatment is highly kurtotic, whereas that for oyster larvae exhibits this central tendency to a much lesser degree. Figure 1 shows the 95 percent confidence limits of the mean ($\pm 2\ SE_m$) in microns, with $N=100$ for oyster larvae and $N=50$ for clam larvae, at the various mean lengths encountered in our experimental cultures.

After considering the variations encountered, in addition to sampling errors, we believe our

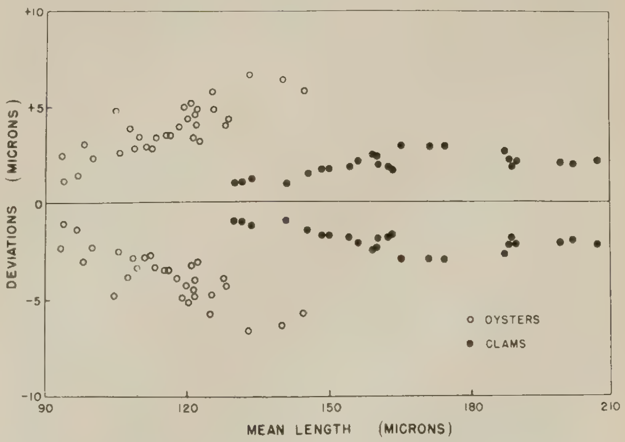

FIGURE 1.—The 95 percent confidence limits of measurements of mean lengths of oyster and clam larvae of different sizes. Values indicate $\pm 2\ SE_m$. $N=100$ for oyster larvae; $N=50$ for clam larvae.

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[3] Trade names referred to in this publication do not imply endorsement of commercial products.

transformed values (G) for measurements of growth are generally accurate to about ±10 percent for oyster larvae and to about ±5 percent for clam larvae. The confidence limits for oyster larvae were not narrowed appreciably even by increasing N to 300; therefore, it was considered impractical to increase the number of measurements of oyster larvae sufficiently to reduce the error to that of measurements of clam larvae.

Errors involved in our techniques for determining numbers of larvae developing from fertilized eggs to straight-hinge larvae or the number surviving in growth experiments have been found to be about ±10 percent.

In any event, the effects of test compounds on larval growth and survival are readily distinguished, from random variation, by the regular stepwise reduction at each successive increase in concentration of the test chemical.

EFFECTS OF DIFFERENT COMPOUNDS ON EMBRYOS AND LARVAE

Table 1 shows the relative percentage of fertilized oyster and clam eggs that developed through normal embryonic stages into straight-hinge larvae, the relative percentage of larvae that survived, and the relative percentage increase in mean length when exposed to various pesticides and chemicals. We calculated the relative percentages, as has been previously stated, by using the survival and rate of growth of larvae in the control cultures of each experiment as 100 percent. The values given (except where noted) are averages for duplicate cultures at each concentration in each experiment. When more than one experiment was run, we combined the results of all experiments.

Some compounds were more toxic to embryos than to larvae (despite the much shorter exposure period of the embryos), although the reverse is generally indicated in our tests. The differences between the tolerance of developing embryos and larvae of oysters to the same pesticide are strikingly evident from the effects of the weedicides, Amitrol and Endothal (table 1). Embryos developed normally in higher concentrations of Amitrol (500 p.p.m.) than those at which larvae showed good growth (100 p.p.m.). In contrast, eggs could tolerate only 10 p.p.m. of Endothal, whereas larvae showed about normal growth at concentrations as high as 50 p.p.m.

The compounds we used in our tests differed widely in chemical composition and presumably have different modes and sites of action. It is not too surprising, therefore, that although the toxic levels of most compounds are about the same for clams and oysters, some are appreciably more toxic to one than to the other. The tolerance of oyster larvae to Endothal, for example, was considerably greater than that of clam larvae (although oyster embryos were slightly less tolerant than were clam embryos). Oyster larvae showed fair survival and normal growth at 25 p.p.m., whereas this concentration caused 100 percent mortality of clam larvae. In general, however, the rates of growth of clam larvae are less affected by toxicants than growth of oyster larvae.

As has been reported previously (Davis, 1960), some of the lower concentrations of certain compounds significantly accelerated growth of larvae (notably Sevin, Endothal, 2-4-D salt, phenol, and Sulmet—table 1). Although the reasons for this phenomenon are not clear, we believe it is the result of the bacteriostatic or, possibly, chelating effect of these compounds. Because growth of clam larvae is less affected by bacterial and algal toxins than is growth of oyster larvae, any bacteriostatic or chelating effect these compounds might have would be expected to have a less marked effect on growth of clam larvae than on growth of oyster larvae.

Synergistic Action of Solvent With Some Compounds

With certain pesticides, the solvent may act as a synergist and increase the toxicity of the compound, but with other pesticides the same solvent may show no such action. Acetone appeared to act as a synergist with Co-Ral but not with Di-Syston and Phygon. In experiments when the stock solutions of these three water-insoluble compounds were made up in acetone (appendix), the pair of control cultures receiving 100 p.p.m. acetone (the maximum concentration used in any of the experimental cultures) showed no significant reduction in growth or survival of either clam or oyster larvae. Survival and growth of clam larvae receiving Di-Syston and Phygon decreased progressively as the concentrations of these compounds increased, just as it did in various concentrations of the water-soluble toxicants (table 1). The toxic effects of Co-Ral, however, show a definite break in the middle of the series that corresponds to the break in acetone concentrations.

To obtain the six concentrations of these acetone-soluble compounds, from 0.25 to 10 p.p.m., we used two stock solutions. The concentrations of 0.25, 0.5, and 1 p.p.m. of toxicants were obtained by increasing volumes of the less concentrated stock solution so that the concentrations of acetone were 25, 50, and 100 p.p.m. The concentrations of 2.5, 5, and 10 p.p.m. were achieved by increasing volumes of the more concentrated stock solution, again giving concentrations of acetone of 25, 50, and 100 p.p.m.

The stepwise decrease in survival and growth of clam larvae at 0.25, 0.5, and 1 p.p.m. Co-Ral, followed by better survival and growth at 2.5 p.p.m. and stepwise reduction at 5 and 10 p.p.m. indicates that the action of Co-Ral was being synergized by the acetone solvent (the action of Di-Syston and Phygon was not). The effect of Aldrin on clam embryos shows some evidence of similar synergism.

Variable Effects of Endrin and Dieldrin

Results of different experiments with these two compounds varied considerably even when acetone stock solutions were used. The results given for endrin and dieldrin, therefore, are the average values of a number of experiments but in some experiments tolerances were significantly below these averages. We assume that the variation in the several experiments was caused by differences in particle size and degree of suspension attained in the test culture, since these compounds are essentially insoluble in water. We would expect field observations on commercial applications to yield conflicting data, depending upon the degree of dispersion attained when the pesticide reaches the water.

Possible Indirect Effect of Compounds Through Food Chain

Ukeles (1962) showed that the tolerance for pesticides of some of the best algal foods for bivalve larvae was considerably lower than the tolerances of the larvae. Therefore, even a concentration of a pesticide that showed no effect on eggs or larvae might, indirectly, if used in the field, markedly reduce the growth of bivalve larvae by killing or preventing reproduction of the algae that serve as foods.

We believe the results given in table 1 are, at least primarily, the direct effect of these compounds on the embryos or larvae themselves because we are not dependent upon reproduction of the algae in our larval cultures. We add the food cells to our experimental cultures daily, and the pesticide would have an indirect effect through the food chain only if it destroyed the food cells. The concentration of Sulmet (sodium sulfamethazine) used routinely as a bactericide in our larval cultures, for example, is sufficient to inhibit or prevent reproduction of the algae used for food, yet it has no adverse effect on growth of larvae under our laboratory conditions of feeding.

Significance of TL_m Values

In table 2 we have listed the 24-hour TL_m (the concentration in p.p.m. that would cause an approximate 50-percent reduction in the number of eggs developing into normal straight-hinge larvae) for oyster and clam eggs. Also listed are the 12-day TL_m for clam larvae and the 14-day TL_m for oyster larvae. We believe the TL_m values listed are of value only for rough comparisons of toxicity because some compounds drastically reduce the rate of growth of larvae at concentrations too low to cause appreciable mortality or may kill embryos at lower concentrations than are required to affect growth or survival of larvae. Both endrin and dieldrin, for example, had 14-day TL_m's for oyster larvae greater than 10 p.p.m., yet either of these compounds, at concentrations of only 1 p.p.m., reduced the rate of growth of these larvae drastically. Other compounds, such as Nemagon, Aldrin, and toxaphene, permitted development of embryos at considerably higher concentrations than those at which the larvae could survive and grow. Conversely, other compounds, such as griseofulvin (on clams) and Endothal (on oysters), almost completely stopped embryonic development at concentrations too low to affect seriously survival and growth of the larvae.

In comparison with the TL_m values given for other species, the rankings of Amitrol, Endothal, Omazene, and Phygon are the same for clam and oyster larvae as Bond, Lewis, and Fryer (1960) found for largemouth bass, *Micropterus salmoides*, and two species of salmon, *Oncorhynchus kisutch* and *O. tshawytscha*. The median tolerance limits for the least tolerant stages in the life cycle of clams and oysters for these compounds, however, were lower than the values given for fish. The 96-hour TL_m for bluegills, *Lepomis macrochirus*, to Co-Ral and Di-Syston, reported by Henderson, Pickering, and Tarzwell (1960), was also higher than that for the least tolerant stages of clams.

NEED FOR FURTHER STUDY

The examples cited indicate the need for evaluating all aspects of toxicity on rapidly growing and changing animals at each stage of their life cycle. The high tolerance of bivalve larvae to some of these pesticides also suggests that compounds can be chosen to control pest species without serious damage to commercial shellfish. Within the series of insecticides, for example, Davis (1960) showed that DDT was much more toxic to oyster larvae than lindane. Similarly, within the series of herbicides tested, Amitrol was "safe" at 100 p.p.m., whereas MCPA caused a significant reduction in the rate of growth of oyster larvae at all concentrations above 0.25 p.p.m. We believe, as Thimann (1964) suggested, that emphasis should be placed on developing "substances whose action is selective and on those which decompose quickly."

TABLE 1.—*Percentage of eggs of American oyster and hard clam that developed normally, percentage of larvae that survived, and percentage increase in mean length, in the presence of different concentrations of chemicals* [1]

Compound	Concentration	Oysters			Clams		
		Eggs developing	Survival of larvae	Increase in length of larvae	Eggs developing	Survival of larvae	Increase in length of larvae
Insecticides:	*P.p.m.*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*
Aldrin (2 experiments; acetone solution)	0.25	----	----	----	96	[2] 75	[2] 20
	.50	----	----	----	90	[2] 37	[2] 9
	1.00	----	----	----	71	0	----
	2.50	----	----	----	86	0	----
	5.00	----	----	----	83	0	----
	10.00	----	----	----	64	0	----
Co-Ral (2 experiments; acetone solution)	.0025	89	74	83	----	----	----
	.0050	100	66	105	----	----	----
	.01	103	87	92	----	----	----
	.025	111	91	88	----	----	----
	.050	98	90	72	----	----	----
	.10	55	95	61	----	----	----
	.25	0	104	49	95	87	89
	.50	0	99	38	97	72	67
	1.00	0	75	17	99	44	39
	2.50	----	----	----	88	74	57
	5.00	----	----	----	87	52	44
	10.00	----	----	----	42	5	14
DDT (1 experiment; water suspension)	.025	----	80	54	----	----	----
	.050	----	0	----	----	----	----
Dicapthon (1 experiment; water solution)	.10	----	----	----	112	91	89
	.20	----	----	----	91	88	87
	1.00	----	----	----	95	89	59
	2.00	----	----	----	60	94	65
	10.00	----	----	----	0	0	----
Dieldrin [3] (4 experiments; 1 water suspension and 3 acetone solution)	.025	95	69	95	----	----	----
	.05	75	68	79	----	----	----
	.10	74	66	67	----	----	----
	.25	67	58	30	----	----	----
	.50	60	59	42	----	----	----
	1.0	29	63	35	----	----	----
	2.5	46	91	37	----	----	----
	5.0	40	84	27	----	----	----
	10.0	31	80	13	----	----	----
Dipterex (1 experiment; water solution)							
	.025	----	----	67	----	----	----
	.050	----	----	78	----	----	----
	1.00	----	50	64	----	----	----
Di-Syston (2 experiments; acetone solution)							
	.025	110	103	106	----	----	----
	.050	98	99	116	----	----	----
	.100	96	115	117	----	----	----
	.25	103	97	101	99	91	98
	.50	82	91	80	92	81	96
	1.00	75	76	51	80	67	74
	2.50	53	64	9	75	2	14
	5.00	56	34	2	52	0	----
	10.00	21	0	----	16	0	----
Endrin [4] (5 experiments; 2 water suspension and 3 acetone solution)							
	.025	103	79	111	----	----	----
	.050	91	67	70	----	----	----
	.100	92	70	61	----	----	----
	.25	52	67	38	----	----	----
	.50	58	66	20	----	----	----
	1.00	44	50	30	----	----	----
	2.5	44	78	35	----	----	----
	5.0	42	79	12	----	----	----
	10.0	48	83	11	----	----	----

See footnotes at end of table.

Table 1.—*Percentage of eggs of American oyster and hard clam that developed normally, percentage of larvae that survived, and percentage increase in mean length, in the presence of different concentrations of chemicals* [1]—Continued

Compound	Concentration	Oysters: Eggs developing	Oysters: Survival of larvae	Oysters: Increase in length of larvae	Clams: Eggs developing	Clams: Survival of larvae	Clams: Increase in length of larvae
Insecticides—Continued	*P.p.m.*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*
Guthion (1 experiment; water solution)	.25	91			106	81	95
	.50	65			109	81	95
	1.00	0			31	38	98
	2.50						
	5.00	0			0	0	
	10.00	0			0	0	
Lindane (1 experiment; water solution)							
	.25	127			97	117	86
	.50	114			112	102	98
	1.00	84			111	100	101
	2.50						
	5.00	82			106	103	107
	10.00	43			60	67	71
Malathion (2 experiments; acetone solution)							
	.25	104	90	86			
	.50	95	88	90			
	1.00	101	66	77			
	2.50	89	52	74			
	5.00	85	20	72			
	10.00	42	3	41			
N-3452 (1 experiment; water solution)							
	.50	0	0				
	1.0	0	0				
	2.5	0	0				
	5.0	0	0				
N-3514 (1 experiment; water solution)							
	1.0	0	0		0	5	30
	10.0	0	0		0	0	
Parathion (1 experiment; water solution)							
	.025			103			
	.050			87			
	1.00			22			
Sevin (3 experiments; 1 water solution and 2 acetone solution)							
	.02	88	111	109	85		
	.025				97		
	.050				100		
	.10	96	113	119	77		
	.20	104	117	124	91		
	1.00	106	119	106	94	103	92
	2.00	90	135	72	77		
	2.50				64	85	30
	4.00	11	0		48		
	5.00				0		
	10.00	0	0		[2] 41		
TEPP (1 experiment; water solution)							
	1.00	100	101	80			
	2.50	91	93	70			
	5.00	100	101	61			
	10.00	74	90	41			
Toxaphene (2 experiments; acetone solution)							
	.25				84	33	21
	.50				91	11	5
	1.00				51	0	
	2.50				39	0	
	5.00				37	0	
	10.00				0	0	
Herbicides:							
Amitrol (2 experiments; water solution)							
	2.50	101	99	117			
	5.00	99	94	111			
	10.00	103	100	96			
	25.00	95	80	117			
	50.00	104	80	112			
	100.00	104	96	116			
	250.00	104	51	71			
	500.00	94	5	36			
	1,000.00	2	0				
Amitrol-T (1 experiment; water solution)							
	.25	93	91	116			
	.50	100	89	107			
	1.00	48	97	109			
	2.50	93	96	105			
	5.00	89	104	99			
	10.00	88	78	108			
2-4-D ester (1 experiment; acetone solution)							
	.025		95	99			
	.05		97	95			
	.10		80	89			
	.25	90	102	70			
	.50	89	98	100			
	1.00	80	0				
	2.50	89					
	5.00	85					
	10.0	27					

See footnotes at end of table.

TABLE 1.—*Percentage of eggs of American oyster and hard clam that developed normally, percentage of larvae that survived, and percentage increase in mean length, in the presence of different concentrations of chemicals* [1]—Continued

Compound	Concentration	Oysters			Clams		
		Eggs developing	Survival of larvae	Increase in length of larvae	Eggs developing	Survival of larvae	Increase in length of larvae
Herbicides—Continued	*P.p.m.*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*
2-4-D salt (2 experiments; water solution)	.025		84	148			
	.05		98	194			
	.10		93	134			
	.25	84	92	124			
	.50	91	89	111			
	1.0	82	102	119			
	2.5	78	103	83			
	5.0	79	112	86			
	10.0	88	97	77			
	25.0	29	104	62			
	50.0	32	52	39			
	100.0	0	45	8			
Diuron (1 experiment; water solution)							
	.25				92	128	99
	.50				91	112	101
	1.00				81	127	94
	5.00				0	[5] 100	62
EMID (4 experiments; water solution)							
	.25	103	99	81			
	.50	101	92	99			
	1.0	107	95	87			
	2.5	101	106	94			
	5.0	101	106	82			
	10.0	90	98	78			
	25.0	2	61	47			
	50.0	0	11	1			
	100.0	0	0				
Endothal (2 experiments; water solution)	.25	95	97	124	98	100	104
	.50	108	98	148	86	104	108
	1.00	101	97	129	85	103	104
	2.50	91	111	130	98	92	99
	5.00	102	109	129	93	91	91
	10.0	94	109	119	89	60	64
	25.0	57	74	96	76	0	
	50.0	1	48	90	51	0	
	100.0	0	2	18	0	0	
Fenuron (2 experiments; water solution)	.025				100	92	[6] 76
	.050				100	53	[6] 64
	.20				100	69	[6] 38
	.25				[7] 91	86	[7] 110
	.50				[7] 92	[7] 75	[7] 115
	1.00				[6,7] 98	[7,8] 95	[7,8] 119
	2.00				[6] 97	[6] 0	[6] 0
	4.00				[6] 98	[6] 0	[6] 0
	5.00				[7] 95	[7] 115	[7] 109
	10.00				[6] 115	[6] 0	[6] 0
MCPA (2 experiments; water solution)	.25	100	75	69			
	.50	103	89	99			
	1.00	99	89	110			
	2.50	94	88	86			
	5.00	96	80	77			
	10.00	80	89	61			
	25.00	0	64	30			
	50.00	0	8	14			
	100.00	0	0				
Monuron (1 experiment; water solution)	.25				93	120	114
	.50				99	122	109
	1.00				91	128	86
	5.00				92	111	93
Neburon (1 experiment; water solution)	2.4				0	0	
	4,8				0	0	
Silvex (1 experiment; acetone solution)							
	.025		89	128			
	.05		101	108			
	.1		99	91			
	.25	100	102	94			
	.50	81	85	38			
	1.0	75	0				
	2.5	78					
	5.0	56					
	10.0	22					
Nematocide:							
Nemagon (2 experiments; acetone solution)							
	.25				100	116	75
	.50				98	97	30
	1.00				100	14	21
	2.50				98	<1	4
	5.00				95	0	
	10.00				86	0	
Solvents:							
Acetone (1 experiment; confirmed by others)							
	10.0	162			91	100	110
	25.0				107	100	104
	50.0	122			98	100	91
	100.0	158			93	100	91
	250.0					100	87

See footnotes at end of table.

TABLE 1.—*Percentage of eggs of American oyster and hard clam that developed normally, percentage of larvae that survived, and percentage increase in mean length, in the presence of different concentrations of chemicals* [1] Continued

Compound	Concentration	Oysters			Clams		
		Eggs developing	Survival of larvae	Increase in length of larvae	Eggs developing	Survival of larvae	Increase in length of larvae
Solvents—Continued	*P.p.m.*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*
Allyl alcohol (1 experiment; water solution)	.25	---	---	---	95	0	---
	.50	---	---	---	76	0	---
	1.0	---	---	---	51	0	---
	2.5	---	---	---	0	0	---
	5.0	---	---	---	0	0	---
	10.0	---	---	---	0	0	---
Orthodichlorobenzene (1 experiment; acetone solution)							
	.25	---	---	---	107	121	95
	.50	---	---	---	94	111	98
	1.0	---	---	---	99	123	92
	2.5	---	---	---	94	107	97
	5.0	---	---	---	106	107	94
	10.0	---	---	---	79	82	86
Trichlorobenzene (1 experiment; acetone solution)							
	1.0	59	---	---	72	108	102
	10.0	21	---	---	58	69	104
Bactericides, fungicides, algicides, miscellaneous:							
Chloramphenicol (1 experiment; water solution)							
	.1	---	---	---	108	97	111
	.2	---	---	---	111	104	117
	1.0	---	---	---	106	84	104
	2.0	---	---	---	100	87	101
	10.0	---	---	---	107	90	81
	100.0	---	---	---	30	0	---
Delrad (1 experiment; water solution)							
	.01	---	94	89	---	117	96
	.05	---	9	50	---	[9] 88	42
	.1	---	0	---	---	0	---
	.2	---	0	---	---	0	---
Dowicide A (1 experiment; water solution)							
	.25	---	---	---	104	70	114
	.50	---	---	---	86	136	119
	1.00	---	---	---	102	0	---
	2.50	---	---	---	100	0	---
	5.00	---	---	---	94	0	---
	10.00	---	---	---	55	0	---
Dowicide G (1 experiment; water solution)							
	.25	---	---	---	0	0	---
	.50	---	---	---	0	0	---
	1.00	---	---	---	0	0	---
	2.50	---	---	---	0	0	---
	5.00	---	---	---	0	0	---
	10.00	---	---	---	0	0	---
Griseofulvin (1 experiment; water solution)							
	.025	---	---	---	---	106	101
	.050	---	---	---	---	94	100
	.10	---	---	---	---	99	109
	.25	---	---	---	36	101	98
	.50	---	---	---	0	105	103
	1.00	---	---	---	0	86	101
	2.50	---	---	---	0	---	---
	5.00	---	---	---	0	---	---
	10.00	---	---	---	0	---	---
PVP-Iodine (2 experiments; water solution)							
	.25	---	---	---	---	99	106
	.50	---	---	---	---	103	101
	1.00	---	---	---	---	108	102
	2.50	---	---	---	108	116	100
	5.00	---	---	---	103	85	97
	10.00	---	---	---	94	92	93
	25.00	---	---	---	1	82	56
	50.00	---	---	---	0	1	9
	100.00	---	---	---	0	---	---
Nabam (1 experiment; water solution)							
	.5	0	---	---	0	118	9
	1.0	0	---	---	0	102	8
	2.5	0	---	---	0	0	---
	5.0	0	---	---	0	0	---
	10.0	0	---	---	0	0	---
Nitrofurazone (1 experiment; water solution)							
	2.50	---	---	---	104	94	97
	5.00	---	---	---	111	101	83
	10.00	---	---	---	111	101	75
	25.00	---	---	---	119	87	53
	50.00	---	---	---	103	93	45
	100.00	---	---	---	102	80	23
Omazene (2 experiments; water solution)							
	.025	87	107	122	101	93	104
	.05	79	103	123	97	91	104
	.10	34	84	112	21	93	98
	.25	0	76	22	0	90	74
	.50	0	0	---	0	12	33
	1.00	0	0	---	0	0	---

See footnotes at end of table.

TABLE 1.—*Percentage of eggs of American oyster and hard clam that developed normally, percentage of larvae that survived, and percentage increase in mean length, in the presence of different concentrations of chemicals* [1]—Continued

Compound	Concentration	Oysters			Clams		
		Eggs developing	Survival of larvae	Increase in length of larvae	Eggs developing	Survival of larvae	Increase in length of larvae
Bactericides—Continued	*P.p.m.*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*
Pentachlorophenol (1 experiment; acetone solution)	.025		115	104			
	.05		86	80			
	.10		0				
	.25	0	0				
	.50	0	0				
	1.00	0					
	2.50	0					
	5.00	0					
Pentachlorophenyl acetate (1 experiment; acetone solution)	.025		41	60			
	.05		0				
	.10		0				
	.25	0	0				
	.50	0	0				
	1.00	0					
	2.50	0					
	5.00	0					
Phenol (1 experiment; water solution)	.025	103			111	121	109
	.05	110			101	131	114
	.10	112			126	143	115
	.20	102			105	130	119
	1.0	103			99	137	125
	2.0	94			113	166	128
	10.0	102			95	149	55
	100.0	5			0	0	
Phygon (2 experiments; acetone solution)	.00025	110	106	100	97	99	99
	.0050	101	113	76	91	99	99
	.01	69	95	39	65	104	96
	.025	0	79	20	1	94	76
	.050	0	32	9	0	58	31
	.10	0	0		0	34	21
	.25				0	0	
	.50				0	0	
	1.00				0	0	
Roccal (1 experiment; water solution)	.1				97	80	86
	.2				45	0	
	1.0				0	0	
Rosin Amine D (1 experiment; acetone solution)	.025		5				
	.05		0				
	.10		0				
	.25	0	0				
	.50	0	0				
	1.00	0					
	2.50	0					
	5.00	0					
Sulmet (1 experiment; water solution of tinted veterinary formula)	.1				103	97	109
	.2				108	113	112
	1.0				111	103	106
	2.0				105	106	87
	10.0				95	113	83
	100.0				107	98	37
Sulmet (1 experiment; water solution of new untinted 1962 formulation)	50.00		90	150		111	97
	100.00		95	155		90	100
	150.00		94	148			
	200.00		108	138		114	101
	300.00		108	131		111	100
	400.00		110	121		108	98
	500.00		112	92		110	96
	600.00		101	72			
	1,000.00					98	85
TCC (1 experiment; water solution)	.0025					106	91
	.005					92	48
	.01					19	5
	.025				69	89	18
	.05				0	7	6
	.1				0	0	
	.25				0		
	.50				0		
	1.00				0		
TCP (1 experiment; water solution)	.025		100	116			
	.05		94	129			
	.10		96	117			
	.25	96	87	116			
	.50	62	99	114			
	1.00	2	85	14			
	2.50	20					
	5.00	0					
	10.00	0					

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[1] Relative percentages calculated by using survival and growth rates of larvae in control cultures.

[2] 1 experiment only.

[3] Results with Dieldrin very erratic (see text).

[4] Results with Endrin very erratic (see text).

[5] 1 culture only; duplicate 97 percent mortality.

[6] 1st experiment.

[7] 2d experiment.

[8] 97 percent mortality in 1st experiment.

[9] 1 culture only; duplicate 100 percent mortality.

TABLE 2.—*Estimated concentrations (TL_m values), calculated by interpolation from data in table 1, at which 50 percent of the eggs of oysters and clams develops normally or 50 percent of the larvae survives*

Compound	Oysters		Clams	
	48-hr. TL_m eggs	14-day TL_m larvae	48-hr. TL_m eggs	12-day TL_m larvae
Insecticides:				
Aldrin			>10.00	0.41
Co-Ral	0.11	>1.00	9.12	5.21
DDT		.034		
Dicapthon			3.34	5.74
Dieldrin	.64	>10.00		
Dipterex		1.00		
Di-Syston	5.86	3.67	5.28	1.39
Endrin	.79	>10.00		
Guthion	.62		.86	.86
Lindane	9.10		>10.00	>10.00
Malathion	9.07	2.66		
N-3452	<.50	<.50		
N-3514	<1.00	<1.00	<1.00	<1.00
Parathion				
Sevin	3.00	3.00	3.82	>2.50
TEPP	>10.00	>10.00		
Toxaphene			1.12	<.25
Herbicides:				
Amitrol	733.70	255.44		
Amitrol-T	>10.00	>10.00		
2-4 D ester	8.00	.74		
2 4-D salt	20.44	64.29		
Diuron			2.53	>5.00
EMID	16.82	30.00		
Endothal	28.22	48.08	51.02	12.50
Fenuron			>10.00	>5.00
MCPA	15.62	31.30		
Monuron			>5.00	>5.00
Neburon			<2.4	<2.4
Silvex	5.90	.71		
Nematocide: Nemagon			10.00	.78
Solvents:				
Acetone	>100.00		>100.00	>100.00
Allyl alcohol			1.03	<.25
Orthodichlorobenzene			>100.00	>100.00
Trichlorobenzene	3.13		>10.00	>10.00
Bactericides, fungicides, algicides, miscellaneous:				
Chloramphenicol			74.29	50.00
Delrad		.031		.072
Dowicide A			>10.00	.75
Dowicide G			<.25	<.25
Griseofulvin			<.25	<1.00
PVP-Iodine			17.10	34.94
Nabam	<.50		<.50	1.75
Nitrofurazone			>100.00	>100.00
Omazene	.078	.34	.081	.378
Pentachlorophenol	<.25	.071		
Pentachlorophenyl acetate	<.25	<.025		
Phenol	58.25		52.63	55.00
Phygon	.014	.041	.014	1.75
Roccal			.19	.14
Rosin Amine D	<.25	<.025		
Sulmet, tinted			>100.00	>100.00
Sulmet, untinted	>600.00	>600.00	>1,000.00	>1,000.00
TCC			.032	.037
TCP	.60	>1.00		

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APPENDIX

Table A-1.—*Source, solubility, and chemical names of compounds tested*

Common name	Chemical name	Solubility in p.p.m.	Source
Insecticides:			
Aldrin	Hexachlorohexahydro-endo, exo-dimethanonaphthalene.	Insoluble in water; 1,590,000 in acetone	Shell Chemical Corp.
Co-Ral	O,O-diethyl O-3-chloro-4-methyl-2-oxo-2H-1-benzopyran-7-yl phosphorothioate.	Insoluble in water; soluble in acetone	Chemagro Corp.
DDT	Dichlorodiphenyltrichloroethane	0.0002 in water (0.2 as colloid); 590,000 in acetone.	
Dicapthon	O-O-dimethyl-O(2 chloro-4 nitrophenyl) phosphorothioate.	Very low solubility in water; very low solubility in acetone.	American Cyanamid Co.
Dieldrin	Hexachloroepoxyoctahydro-endo, exo-dimethanonaphthalene.	Insoluble in water; 540,000 in acetone	Shell Chemical Corp.
Dipterex	O,O-dimethyl-1-hydroxy-2,2,2-trichloroethyl-phosphonate.	130,000 in water	Chemagro Corp.
Di-Syston	O,O-diethyl S-2-(ethylthio)ethyl phosphorodithioate.	25 in water; soluble in acetone	Do.
Endrin	Hexachloroepoxyoctahydro-endo, endo-dimethanonaphthalene.	"Insoluble" in water; "moderately" soluble in acetone.	Shell Chemical Corp.
Guthion	O,O-dimethyl S-4-oxo-1,2,3-benzotriazino-3(4H)-ylmethyl phosphorodithioate.	33 in water	Chemagro Corp.
Lindane	1,2,3,4,5,6-hexachlorocyclohexane	10 in water; 440,000 in acetone	Niagara Chemicals Division, Food Mach. & Chem. Corp.
Malathion	O,O-dimethyl dithiophosphate of diethyl mercaptosuccinate.		American Cyanamid Co.
N-3452	Alkyl (C_8 C_{18}) dimethyl benzyl ammonium chloride.		Niagara Chemicals Division, Food Mach. & Chem. Corp.
N-3514	2-chloro-1-nitropropane.	8,000 in water	Do.
Parathion	O,O-diethyl O-p-nitrophenyl thiophosphate.	20 in water	Chemagro Corp.
Sevin	1-naphthyl-N-methylcarbamate	1,000 in water; 300,000 in acetone	Union Carbide Chem. Co.
TEPP	Tetraethyl pyrophosphate	Miscible in water (hydrolyzes); miscible in acetone.	Niagara Chemicals Division, Food Mach. & Chem. Corp.
Toxaphene	Mixture of polychloro bicyclic terpenes with chlorinated camphene predominating.	1.5 in water; 4,500,000 in acetone	Hercules Powder Co.
Herbicides:			
"Amitrol" Aminotriazole	3-amino-1H-1,2,4-triazole	Very soluble in water	
Amitrol-T	3-amino-1H-1,2,4-triazole with ammonium thiocyanate.	do.	
2-4-D ester	Butoxyethanol ester of (2,4-dichlorophenoxy) acetic acid.	"Insoluble" in water.	Thompson Hayward Chemical Co.
2-4-D salt	Dimethylamine salt of (2,4-dichlorophenoxy)acetic acid.	Very soluble in water	Do.
Diuron	3-(3,4-dichlorophenyl)-1,1-dimethylurea	42 in water	E. I. duPont de Nemours & Co.
EMID	2,4-dichlorophenoxy-acetamide	Very soluble in water	
Endothal	Disodium 3,6-endoxohexahydrophthalate	280,000 in water	Pennsalt Chemical Co.
Fenuron	3 phenyl-1,1-dimethylurea	2,900 in water	E. I. duPont de Nemours & Co.
MCPA	Dimethylamine salt of (2-methyl-4-chlorophenoxy) acetic acid.	Very soluble in water	American Chemical Paints Co.
Monuron	3-(p-chlorophenyl)-1, 1-dimethylurea	230 in water.	E. I. duPont de Nemours & Co.
Neburon	1-n-butyl-3-(3,4-dichlorophenyl)-1-methylurea.	4.8 in water	Do.
Silvex	Butoxyethanol ester of (2,4,5-trichlorophenoxy)propionic acid.	0.014 percent in water; 15.2 percent in acetone.	
Nematocide:			
Nemagon	1,2-dibromo-3-chloropropane	1,000 in water; very soluble in acetone	Shell Chemical Corp.
Solvents:			
Acetone	Acetone.	Miscible in water	Mallinckrodt Chemical Works.
Allyl alcohol.	Propen-1-ol-3	do	Shell Chemical Corp.
Orthodichlorobenzene	o-dichlorobenzene.	130 in water; miscible in acetone	Niagara Chemicals Division, Food Mach. & Chem. Corp.
Trichlorobenzene	Trichlorobenzene	25 in water; miscible in acetone	Do.
Bactericides, fungicides, algicides, miscellaneous:			
Chloramphenicol	(Chloromycetin) D-(-)-threo-2-dichloroacetamido-1-p-nitrophenyl-1,3-propanediol.	2,500 in water; very soluble in acetone	Parke, Davis & Co.
Delrad	Dehydro-abietylamine acetate	Very soluble in water	Hercules Powder Co.
Dowicide A	O-phenylphenol, sodium salt	1,220,000 in water	Dow Chemical Co.
Dowicide G	Sodium pentachlorophenate, technical	330,000 in water	Do.
Griseofulvin	7-chloro-2′,4,6-trimethoxy-6′-methylspiro[benzofuran-2(3H),1′-[2]cyclohexene]-3,4-dione.	10.0 in water	McNeil Laboratories, Inc.
PVP-Iodine.	Polyvinylpyrrolidone-iodine complex	Very soluble in water	Antara Chemicals Division, General Analine & Film Corp.
Nabam.	Disodium ethylenebis(dithiocarbamate)	do	Niagara Chemicals Division, Food Mach. & Chem. Corp.
Nitrofurazone	5-nitro-2-furaldehyde semicarbazone	238 in water	Hess Clark Division, Vick Chemical Co.
Omazene	Copper dihydrazinium sulfate	"Very slightly" soluble in water	Olin Mathieson Chemical Corp.
Pentachlorophenol	Pentachlorophenol.	80 in water; very soluble in acetone	Monsanto Chemical Co.
Pentachlorophenyl acetate	Pentachlorophenyl acetate		Niagara Chemicals Division, Food Mach. & Chem. Corp.
Phenol	Phenol	82,000 in water; very soluble in acetone.	Mallinckrodt Chemical Works.
Phygon.	2,3-dichloro-1,4-naphthoquinone	"Insoluble" in water	Niagara Chemicals Division, Food Mach. & Chem. Corp.
Roccal	Alkyl (C_8H_{17}–$C_{18}H_{37}$)dimethylbenzyl-ammonium chloride.	10 percent solution; very soluble in water.	Sterwin Chemicals, Inc.
Rosin Amine D	Rosin amine D (technical grade of dehydroabietylamine).	"Insoluble" in water; very soluble in acetone.	Hercules Powder Co.
Sulmet (tinted veterinary soluble).	(Sodium sulfamethazine)sodium(4,6-dimethyl-2-sulfanilamidopyramidine).	Very soluble in water	Agricultural Division, American Cyanamid Co.
Sulmet (untinted soluble)	do	do	Do.
"TCC"	3,4,4′-trichlorocarbanilide	"Insoluble" in water; 40,000 in acetone.	Monsanto Chemical Co.
2,4,5 TCCPA	Propylene glycol to butyl ether esters of 2-(2,4,5-trichlorophenoxy)propionic acid.		

BIOLOGICAL STUDIES AND ESTIMATES OF OPTIMUM ESCAPEMENTS OF SOCKEYE SALMON IN THE MAJOR RIVER SYSTEMS IN SOUTHWESTERN ALASKA

By Robert L. Burgner, Charles J. DiCostanzo, Robert J. Ellis, George Y. Harry, Jr., Wilbur L. Hartman, Orra E. Kerns, Jr., Ole A. Mathisen, and William F. Royce[1]

ABSTRACT

An intensive research program was conducted in 1961 and 1962 by the Bureau of Commercial Fisheries Biological Laboratory, Auke Bay, Alaska, and the Fisheries Research Institute, University of Washington, with the cooperation of the Alaska Department of Fish and Game. Many sockeye salmon river systems were studied concurrently with essentially the same techniques so that systems covering the entire range of production levels could be compared. The general objective of this research was to determine the optimum escapement of sockeye salmon for each of the major systems. This was accomplished through integration of the results of several related studies: (1) summarization and analysis of historical and current data on runs of adult sockeye salmon, (2) delineation and description of spawning areas and estimation of their capacities, (3) delineation and description of the nursery areas and estimation of their capacities.

The major systems studied were the Wood, Kvichak, Naknek, and Ugashik systems, which enter Bristol Bay; the Chignik system, on the south side of the Alaska Peninsula; and the Karluk system, on Kodiak Island. Adult sockeye salmon in the commercial catches and escapements, and sockeye salmon smolts, were counted and sampled. Spawning grounds were surveyed to determine their size and quality and the distribution and abundance of spawners. Bathymetric maps were prepared for some of the nursery lakes. Intensive limnological studies, including a major effort to measure primary productivity, were made on many nursery lakes. Several types of gear sampled juvenile sockeye salmon and associated species in the lakes. Interim optimum or target escapements required for highest production on a sustained-yield basis have been established for each major system.

The major task that the manager of a salmon fishery must undertake each year is to set a target escapement of fish to the spawning grounds for each salmon run (stock) under his management. He must have such a goal as a basis for numerous decisions that control the actual time, place, and method of fishing.

A correct decision is extremely valuable. The number of sockeye salmon *(Oncorhynchus nerka)* returning to a single river in Alaska may exceed 20 million in a single year, and each fish caught may be worth as much as $3 after being canned. Sometimes the number of adults returning to a system is much larger than the needed escapement; sometimes it is not large enough. Great year-to-year variability in the size of the run to a given system is common.

The manager must divide the return between catch and escapement, and he must do so in a way that ensures maximum sustainable yield. He must know the optimum escapement and then he must set a target escapement, having in mind the optimum and any modifications that may be indicated by the expected characteristics of the returning run and the expected conditions within the spawning and nursery areas. He will tend to set an escapement slightly higher than the optimum because his control of the fishery is not precise, and he is aware that the cost of slight underfishing is probably less than the cost of slight overfishing. In this way he attempts to make full use of the spawning and nursery areas.

The optimum escapement is usually considered to be the number of adults that will yield the greatest surplus of expected return over needed escapement. The optimum escapement is determined from the historical relation between

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recruitment, which usually is measured as the number of adults returning, and the parent escapement. A simplified example of this relation, developed partly from inference and partly from observation, is a curve that starts at zero and rises to the left of the replacement line (the 45° line representing replacement reproduction at various levels of escapement), so that over a considerable range of escapements the expected return is greater than the parent escapement (fig. 1). The distance between the curve and the replacement line represents surplus production. The curve, however, either levels off or declines because the capacities of the spawning area, the nursery area, or the ocean feeding ground have been exceeded; and an increased number of spawners will not increase the expected return.

In practice, a satisfactory curve is difficult to obtain. First, observations over many years that include values for the entire range of escapement sizes are needed for each run. These observations are not available for most runs in southwestern Alaska. Attempts to estimate the escapement on the basis of the catch per unit of effort of the fishery (International North Pacific Fisheries Commission, 1962) yielded uncertain results because the relation between the catch per unit of effort and the level of the escapement varied with changing gear, changing management practices, and changing effects of competition between units of gear.

Data on the catches of sockeye salmon from runs to Bristol Bay since 1955 present a special problem. The Japanese fishing fleet has intercepted parts of these runs at sea, and its catches in some years have nearly equaled those of United States fishermen in Bristol Bay. The total Japanese catch of Bristol Bay sockeye salmon is not known with reasonable accuracy, and we have no breakdown of their catch by river system.

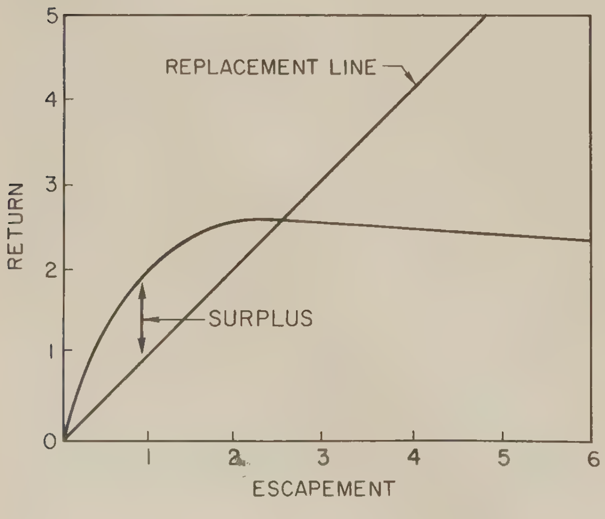

FIGURE 1.—Theoretical return-escapement relation of sockeye salmon.

Even when accurate catch and escapement data have been available, the relation between return and escapement has not been clearly defined—partly because of the cyclic nature of many sockeye salmon runs and partly because survival rates are greatly influenced by environmental conditions which differ from year to year. Obviously, it is desirable to measure abundance before the adults enter the fishery, particularly after completion of any critical part of the life cycle or residence in an environment that may limit production. The mortality of sockeye salmon in fresh water, from potential egg deposition to seaward-migrating smolt, is high and extremely variable; considerable evidence indicates that the fresh water rather than the marine environment usually places upper limits on the numbers of returning adults.

Thus, an important question is: What factors in the fresh-water environment are limiting the size of the sockeye salmon population in each system? First, the adult salmon must have access to spawning areas, and in some systems lack of access may be the limiting factor. Next, the spawning area must have gravel and water suitable for spawning and incubation of the eggs and for sheltering the fry until they emerge. Then, the young fish must find food and shelter for 1 or 2 years in the lake while they grow from a length of about 2.5 cm. to 7 to 13 cm.—smolt size. Finally, the smolts must be able to migrate successfully to sea.

In the sockeye salmon systems of southwestern Alaska, neither the adult's access to the spawning area nor the smolt's path of migration to the sea is restricted. It seems most logical, therefore, to seek limiting factors either during the salmon's life on the spawning grounds as adult, egg, larva, or fry or during its life in the lake as a growing juvenile. Our studies were planned on this assumption, and our task has been to determine approximately the number of spawners that can be expected to produce enough young to fully use the environment.

This report summarizes the data we now recognize as bearing on the question of optimum escapement. In it we recommend (where possible) optimum escapement for each of the sockeye salmon river systems in southwestern Alaska and discuss the factors that affect those levels. The recommendations are the best that we can prepare at this time. They are not the last word—that must await a more detailed understanding of the life of young sockeye salmon.

Commercial fishing for sockeye salmon in southwestern Alaska started in 1884, and the annual catch rose rapidly to more than 10 million fish by 1900 and was rarely less than this until after 1940.[2] Between 1913 and 1938 the annual production in the Bristol Bay area alone exceeded 20 million fish 10 times. The record of 24,700,000 was in 1938. More than half of the catch usually came from the Naknek-Kvichak district, where the fishery produced a record catch of almost 21 million fish in 1938.

During many of the years that the Federal Government managed the sockeye salmon fisheries of southwestern Alaska, desired escapements in the major river systems were established by law. The White Act of June 26, 1924, declared the intent of Congress to limit the catch to 50 percent of the returning salmon—that is, one fish in the escapement for each one in the catch. As our knowledge of the life history of sockeye salmon increased, it became apparent that in some years the stocks were so small that the entire returns were not adequate to use fully the spawning grounds or nursery areas; in other years the returns were so large that escapements of 50 percent were obviously excessive. This provision of the act was repealed on September 4, 1957.[3]

In autumn 1960 it became evident that a major research program was needed to supply additional biological information to be used in the management of the sockeye salmon and pink salmon *(O. gorbuscha)* of Alaska.

This need for information was emphasized by the escapement of more than 3 million adult sockeye salmon to the rivers of the Nushagak fishing district and more than 2 million to the Naknek River in 1959, and an escapement of almost 15 million to the Kvichak River in 1960. These possibly excessive escapements again raised many questions about optimum escapements. In spring 1961, the Secretary of the U.S. Department of the Interior submitted a revised budget in which he requested an increase of \$1½ million for an intensified salmon research program in Alaska.

The study of sockeye salmon was undertaken by the BCF (Bureau of Commercial Fisheries Auke Bay Biological Laboratory). About half the funds and research were contracted to the FRI (Fisheries Research Institute, University of Washington). The two agencies together planned several projects on the major sockeye salmon systems.[4] Both organizations had historically worked in specific sockeye salmon river systems; they concentrated their efforts in these areas during this study. The FRI worked on the systems tributary to Nushagak Bay (the Igushik, Snake, Wood, and Nuyakuk systems) on the mainland, the Kvichak system at the head of the Alaska Peninsula, and the Chignik system on the Gulf of Alaska side of the Peninsula. The BCF worked on the Alagnak, Naknek, Egegik, and Ugashik systems of the Alaska Peninsula and the Karluk system on Kodiak Island (fig. 2). By mutual agreement, one agency or the other analyzed historic records of catch and escapement for individual systems.

The intensified program began in April 1961, and field work continued through the summer of 1962. Most of the techniques used by the two organizations were standardized. Field research guides and standardized data sheets were prepared.

The satisfactory execution of this large program required the effort of many biologists. The research responsibilities within the BCF and FRI were as follows.

For the BCF—George Y. Harry, Jr., and Charles J. DiCostanzo, assisted by Wilbur L. Hartman, were responsible for general planning and supervision. DiCostanzo directly supervised the compilation and analysis of the data on the historical and current catch and escapement of adults and on the records of counts of smolts. Hartman supervised the limnological research

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[2] Extensive statistics on the catch and pack are available in Rich and Ball (1928), Simpson (1960), and in annual publications such as the Pacific Fisherman Yearbook and the Statistical Yearbook of the International North Pacific Fisheries Commission.

[3] Public Law 85–296.

[4] Each lake or group of connected lakes and its outlet to the ocean is termed a "system" and designated in this report by the name of the outlet or trunk river. For example, Amanka and Ualik Lakes are connected to the ocean through the Igushik River, and the system is, therefore, called the Igushik.

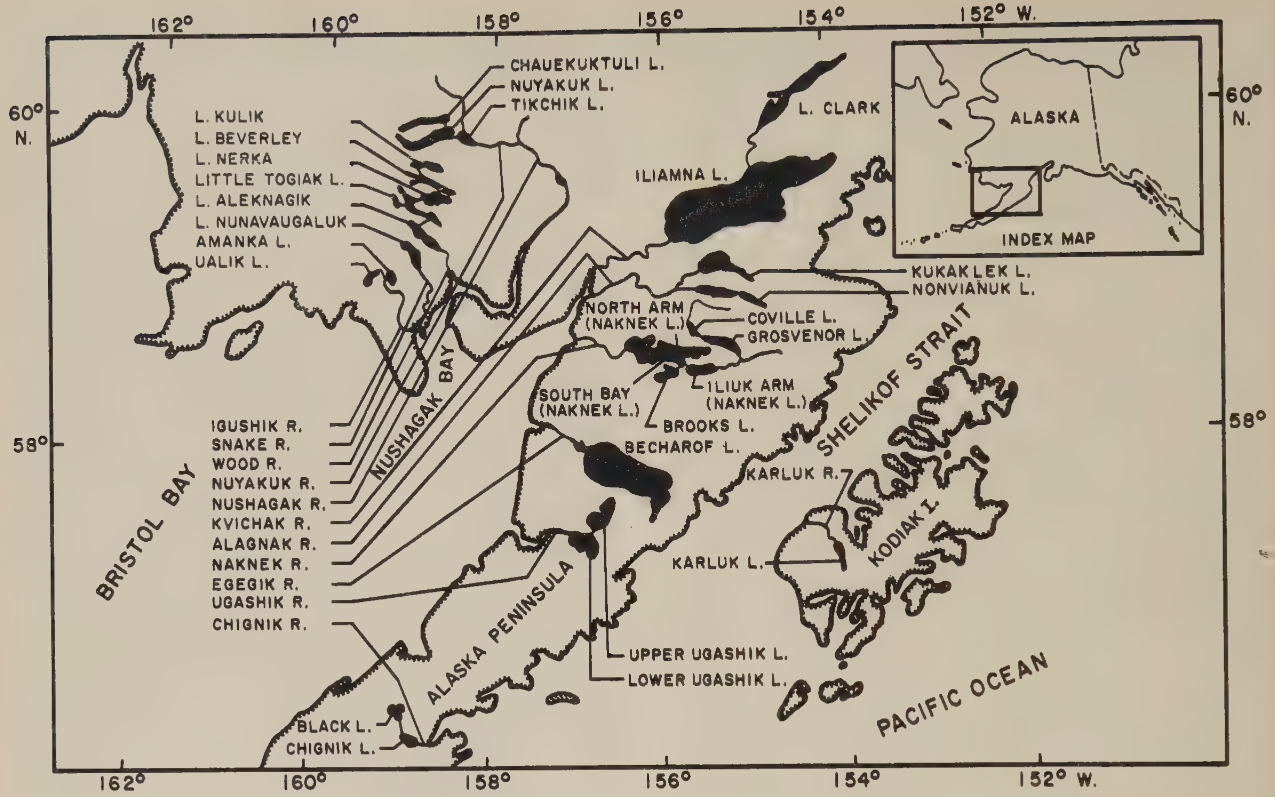
162°
160°
158°
156°
154°
152° W.
60° N.
58°
CHAUEKUKTULI L.
NUYAKUK L.
TIKCHIK L.
L. KULIK
L. BEVERLEY
L. NERKA
LITTLE TOGIAK L.
L. ALEKNAGIK
L. NUNAVAUGALUK
AMANKA L.
UALIK L.
L. CLARK
ILIAMNA L.
ALASKA
INDEX MAP
KUKAKLEK L.
NONVIANUK L.
NORTH ARM (NAKNEK L.)
COVILLE L.
GROSVENOR L.
ILIUK ARM (NAKNEK L.)
SOUTH BAY (NAKNEK L.)
BROOKS L.
BECHAROF L.
SHELIKOF STRAIT
NUSHAGAK BAY
IGUSHIK R.
SNAKE R.
WOOD R.
NUYAKUK R.
NUSHAGAK R.
KVICHAK R.
ALAGNAK R.
NAKNEK R.
EGEGIK R.
UGASHIK R.
CHIGNIK R.
BRISTOL BAY
KARLUK R.
KARLUK L.
KODIAK I.
ALASKA PENINSULA
UPPER UGASHIK L.
LOWER UGASHIK L.
PACIFIC OCEAN
BLACK L.
CHIGNIK L.

FIGURE 2.—Southwestern Alaska, showing major sockeye salmon river systems.

and assisted in studies of spawning ground capacities. John B. Owen helped compile and analyze historical and current records of catch and escapement. Herbert W. Jaenicke was responsible for counting smolts. Robert J. Ellis, William R. Heard, and Benson Drucker supervised studies of young fish. Ellis also assisted in studies of the spawning ground capacities. Richard Straty was responsible for studies of the timing of the migration of spawning fish in the Naknek system.

For the FRI—William F. Royce, Robert L. Burgner, and Ole A. Mathisen were responsible for general planning and supervision. Burgner and Ted S. Y. Koo supervised studies on the systems tributary to Nushagak Bay. Donald Rogers assisted in studies of the rearing areas in the systems tributary to Nushagak Bay. Mathisen, assisted by Orra E. Kerns, supervised studies on the Kvichak system. Royce supervised the studies of David Narver on the Chignik system.

Biologists who performed the research in each area compiled and analyzed the data on the historical and current catch and escapement in that area.

The Alaska Department of Fish and Game provided samples of scales and data for recent years on catch and escapement, length frequency of adults in escapements for many of the rivers, distribution of escapement for the Nushagak fishing district for 1960-62, and lengths, ages, and numbers of smolts for some rivers.

The broad aim of the intensified study of sockeye salmon was to determine the optimum escapement for each of the major systems in southwestern Alaska. In planning the investigation, we recognized that in the short time available little progress toward attaining our goal could be made by a detailed study of a single lake or river system. General principles applicable to each lake or system could be developed more rapidly by comparing the major sockeye salmon systems with respect to their salmon production and the factors in the spawning grounds or lakes that might limit this production. The bases for comparison were as follows: (1) type, quality, amount, and capacity of spawning areas; (2) type, quality, amount, and capacity of nursery areas; and (3) history and characteristics of sockeye salmon runs. Not all aspects of the three categories are discussed for all of the systems because for some systems the data are too few.

PHYSICAL DESCRIPTION OF THE LAKES

A substantial portion of this study was devoted to obtaining physical data on the lakes of sockeye salmon systems in southwestern Alaska. All of these lakes were either formed or modified by glaciation during the Pleistocene (Mertie, 1938; Keller and Reiser, 1959). Except for the Alagnak system, the lakes lie at elevations less than 100 m. above sea level (table 1). In some systems tidal influence extends to or almost to the outlet of the lowest lake.

On the basis of geological and biological aspects, the systems studied fall into two general groups—"Mainland" and "Peninsula." The Mainland Systems drain into Bristol Bay along the west and north shores and include the Igushik, Snake, Wood, Nuyakuk, and Kvichak. Several of the Peninsula Systems enter Bristol Bay from the northeast and east—the Alagnak, Naknek, Egegik, and Ugashik. Two other systems that we place in the peninsula category enter the Pacific Ocean—the Chignik on the east coast of the Alaska Peninsula and the Karluk on the northwest shore of Kodiak Island.

The geology of each general area is believed to be at least partly responsible for differences in water quality. Drainage areas of the Mainland Systems consist primarily of sedimentary rocks, which occasionally include local deposits of limestone. Minor bodies of igneous rocks and other products of volcanism also occur. In contrast, the drainage areas of the Peninsula Systems,

TABLE 1.—*Morphometry and altitudes of major sockeye salmon lakes of southwestern Alaska*

System and lake	Lake area	Depth		Volume	Development of shoreline[1]	Altitude
		Maximum	Mean			
MAINLAND SYSTEMS	*Km.*^{2}	*M.*	*M.*	*Km.*^{3}		*M.*
Igushik system						
Amanka Lake	35	65	23	0.80	3.94	9
Ualik Lake	39	72	28	1.10	1.78	15
Total	74					
Snake system						
Lake Nunavaugaluk	89	162	57	5.10	1.94	14
Total	89					
Wood system						
Lake Aleknagik	83	110	43	3.57	4.22	10
Lake Nerka	201	164	39	7.84	5.70	21
Lake Beverley	90	188	55	4.95	3.46	30
Lake Kulik	45	160	77	3.47	2.80	43
Little Togiak Lake	6	77	30	.18	3.50	23
Total	425			20.01		
Nuyakuk (Tikchik) system						
Tikchik Lake	53	45	15	.80	2.44	95
Nuyakuk Lake	144	283	113	16.27	2.92	95
Lake Chauekuktuli	82	268	111	8.94	2.83	98
Total	279			26.01		
MAINLAND SYSTEMS—Continued	*Km.*^{2}	*M.*	*M.*	*Km.*^{3}		*M.*
Kvichak system						
Iliamna Lake	2,622	301	44	115.81	2.75	15
Lake Clark	267	262	103	27.34	3.60	67
Total	2,889			142.65		
PENINSULA SYSTEMS						
Alagnak (Branch) system						
Kukaklek Lake	176				2.13	246
Nonvianuk Lake	121				1.95	192
Total	297					
Naknek system						
Coville Lake	33	53	19	.64	1.86	33
Grosvenor Lake	73	107	50	3.68	2.54	31
Naknek Lake						
North Arm	182	167	63	11.52	2.07	10
Iliuk Arm	94	173	96	9.00	1.71	10
South Bay	32	71	27	.86	1.41	10
West End	302	80	13	3.77	1.82	10
Brooks Lake	75	79	45	3.39	1.70	19
Total	790			32.86		
Egegik system						
Becharof Lake	1,132				2.26	15
Total	1,132					
Ugashik system						
Upper Ugashik Lake	208				1.72	3
Lower Ugashik Lake	177				1.70	3
Total	385					
Chignik system						
Chignik Lake	22	64	26	.60	2.40	5
Black Lake	39	6	3	.10	1.56	15
Total	61			.70		
Karluk system						
Karluk Lake	40	126	49	1.92	2.01	106
Total	40			1.92		

[1] Ratio of the length of the shoreline to the length of the circumference of a circle of area equal to that of the lake.

although containing sedimentary rocks, have proportionally much more igneous material (Keller and Reiser, 1959). The Alaska Peninsula is an area of current and historical volcanism, and drainages of the Peninsula Systems (including the Karluk) contain many deposits of volcanic ash.

The differences in seasonal changes of water level and turbidity in the lakes are also partly due to differences in geology. Water levels are lowest in the winter in all the systems. Because lakes of systems tributary to Nushagak Bay and those of the Chignik and Karluk systems receive most of their water from snowmelt and rainfall, water levels are highest during spring thaw and autumn rainy periods. In contrast, lakes of the other Peninsula Systems and of the Kvichak system are low in the spring and tend to rise during the summer because of melting ice fields and glaciers. Turbidity often varies widely among the lakes within a system because of the localized source of rock flour carried by glacial meltwater. Turbidity is highest during the summer, especially in lakes that receive glacial melt.

The sockeye salmon lakes in southwestern Alaska differ considerably in the length of their ice-free periods, and presumably the growing season also differs. In general, the lakes of the Mainland Systems that are farther from the influence of the oceanic climate have shorter ice-free periods than lakes nearer the coast. For instance, the lakes of the Nuyakuk system are farthest from the coast and are the last to become ice-free in the spring. The upper lakes of the Wood system do not usually become ice-free until after June 1, whereas Lake Aleknagik, the lowest lake in the Wood system, is usually free of ice during late May. In the Kvichak system, Iliamna Lake, because of its large size and greater exposure to ocean storms, loses its ice cover earlier and forms it later than Lake Clark. Breakup generally occurs by mid-May in Iliamna Lake, which occasionally has areas free of ice during mild weather in the winter.

Lakes of the Peninsula Systems, which are more influenced by the oceanic climate and generally more exposed to wind action, may be ice-free over long periods during the winter. The ice in the Naknek system generally breaks up in early May. Iliuk Arm seldom freezes over completely, and the other Naknek lakes frequently develop areas of open water during mild winters. Lakes of the Egegik and Ugashik systems, which are farther down the peninsula, freeze later (if at all) than the Naknek lakes, and the ice (if any) breaks up earlier. In the Chignik system the shallower lake, Black Lake, is free of ice sooner in the spring than Chignik Lake. Both lakes are generally open by early May and frequently develop areas of open water in the winter. The Karluk system is strongly influenced by the oceanic climate; the ice in Karluk Lake frequently begins to break up in April. The lake occasionally remains ice-free during mild winters.

The two lakes in the Igushik system, Amanka and Ualik, have similar areas, maximum and mean depths, and volumes but have different shoreline developments. Lake Amanka has two distinct basins, which are separated by a sill, but Ualik Lake has a single basin. The Kathlene River flows from Ualik Lake into Amanka Lake and enters the latter in its outlet basin.

Lake Nunavaugaluk, the single lake in the Snake system, is relatively deep and has only one basin and a relatively low shoreline development.

The four main lakes of the Wood system (excluding Little Togiak) are similar in average depth and shoreline development (if Lake Nerka is considered to be two separate lakes joined at their west ends). The deep end of each lake is to the west among the mountains, and the shallower east end extends into lowlands. All of the lakes have altitudes of less than 50 m. (table 1).

The lakes of the Nuyakuk system contrast in size and form. Tikchik Lake is relatively shallow. Lakes Chauekuktuli and Nuyakuk are larger and extremely deep—each has a mean depth of about 112 m. and a cryptodepression that exceeds 170 m.

The two major lakes of the Kvichak system are sharply dissimilar in size and other morphometric characters. Iliamna Lake is the largest body of fresh water in Alaska. Its east end lies among the mountains and has a deeply scoured basin with an irregular shoreline, and because of the many islands and bays, it has a high shoreline development value. The western two-thirds of the lake is relatively shallow and uniform in depth and has few islands and a low shoreline development. Lake Clark, much the smaller of the two major lakes of the system, empties into Iliamna Lake through the Newhalen River. It lies in a long deeply glaciated valley and has a moderately high shoreline development, similar to the average of Iliamna Lake.

The Naknek system contains seven major interconnected lakes or basins all formed by glacial action. In general, the basins are elongate, deep, and steep sided. Within these basins, however, are representatives of most of the major physical and biological types of sockeye salmon lakes in southwestern Alaska. One exception is the lack of a basin as shallow and eutrophic as Black Lake of the Chignik system.

Three lakes of the Naknek system—Coville, Grosvenor, and Naknek—form a chain that drains through Naknek River into Bristol Bay. Coville Lake has the shallowest basin—mean depth, 19 m. It receives a great part of its water from snowmelt and runoff via 80-km.-long American Creek. Coville Lake acts as a settling basin for downstream Grosvenor Lake. Iliuk Arm of Naknek Lake receives drainage from Grosvenor Lake and from glacier fields via the Savonoski River, and from areas of volcanic ash and pumice in the Valley of Ten Thousand Smokes via the Ukak River. The heavy load of rock flour and volcanic materials from these drainages has a profound effect on the water quality and transparency of Iliuk Arm, and to a lesser extent on other areas of Naknek Lake. The South Bay basin of Naknek Lake receives water from Iliuk Arm and North Arm directly, and from Brooks Lake via 1.6-km.-long Brooks River. Brooks Lake receives snowmelt and runoff drainage from low mountains and extensive lowland wet tundra; the water is extremely clear. The North Arm basin of Naknek Lake has a restricted connection to South Bay because of a moraine that forms islands and shallow water along their common border. Drainage into North Arm is snowmelt and runoff, predominantly from areas of wet tundra. The west end of Naknek Lake leading to the outlet is less than 15 m. deep. The comparatively small and shallow northwest basin is separated from North Arm by a moraine and connected to the west end of Naknek Lake across a wide shoal.

Little is known about the morphometry of the remaining lakes in the Bristol Bay area. For lakes of the Alagnak, Egegik, and Ugashik systems we have only the information available from U.S. Geological Survey topographic maps.

The morphometry of the two major lakes of the Chignik system, Chignik and Black, is contrasting. Maximum and mean depths are only 6 and 3 m. for Black Lake, but they are 64 and 26 m. for Chignik Lake. Black Lake flows into Chignik Lake through Black River. Meltwater from an ice field on Mt. Veniaminoff enters Black River and, subsequently, Chignik Lake.

The Karluk system drains via Karluk River into Shelikof Strait on the northwest side of Kodiak Island. The system contains two small lakes and one large lake. The small lakes, Thumb and O'Malley, drain into separate basins of the large lake, Karluk. Karluk Lake is about 20 km. long, has a mean depth of 49 m., and appears to be of glacial origin. Drainage is snowmelt and runoff from a watershed composed predominantly of sedimentary rock.

LIMNOLOGY OF THE LAKES

The limnological studies were designed to help explain why the various lakes and systems produce salmon at different rates. In addition to morphometry of the lakes, we measured factors that other investigators have related to the biological productivity of lakes—chemical and thermal characteristics of the water. We measured biological productivity in terms of primary productivity and the standing crop of phytoplankton. The several measures of water chemistry and biological productivity are examined in relation to production of salmon.

WATER CHEMISTRY

The euphotic zones of the major sockeye salmon nursery lakes were sampled between May 1961 and November 1962 to determine their chemical characteristics. The number of determinations varies among characteristics and lakes, but sampling was concentrated in the more important systems (table 2). Standard methods of collection and analysis were used. In general, lakes of the Peninsula Systems contained higher concentrations of dissolved minerals than those of the Mainland Systems (table 3).

Total Dissolved Solids, Alkalinity, and pH

We have ranked the lakes according to total dissolved solids, total alkalinity, and pH (table 4). As would be expected, the rankings of the lakes by the three measurements tend to be similar, i.e., the more alkaline lakes tended to have higher total dissolved solids and generally higher pH values. Lakes of the Naknek, Chignik, Nuyakuk, and Karluk systems rank highest in total dissolved solids, and those of the Igushik and Snake systems rank lowest. Usually the values for the three characteristics were similar in all of the lakes of a system. The concentrations of total dissolved solids in other deep-water lakes in the Northern Hemisphere (reported by Hutchinson, 1957) are generally higher than the values in sockeye salmon lakes of southwestern Alaska.

Several investigators have used total dissolved solids to predict lake productivity (cf. Larkin and Northcote, 1958; Rawson, 1942, 1961). A comparison of this characteristic with measures of lake productivity is made later.

TABLE 2.—*Months and depths of sampling and numbers of determinations of temperature and various chemical characteristics of sockeye salmon nursery lakes of southwestern Alaska, 1961-62*

System and lake	Month of sampling	Depth sampled	Determinations made					
			O_2	Temperature	Alkalinity	pH	Total dissolved solids	Mineral analysis
MAINLAND SYSTEMS		*M.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*
Igushik system								
Amanka Lake	Aug.	0–25	2	24	-----		2	2
Ualik Lake	Aug.	0–25	2	36	4	4	2	2
Snake system								
Lake Nunavaugaluk	Aug.	0–45	0	16	4	4	2	2
Wood system								
Lake Aleknagik	June-Oct.	0–45	34	192	52	52	10	10
Lake Nerka	June-Oct.	0–45	172	1,915	175	175	14	14
Lake Beverley	June-Oct.	0–45	21	194	26	26	8	8
Lake Kulik	June-Oct.	0–45	25	221	26	26	8	8
Little Togiak Lake	June-Oct.	0–45	34	225	30	30	7	7
Nuyakuk (Tikchik) system								
Tikchik Lake	Aug.	0–30	1	30	4	4	2	2
Nuyakuk Lake	Aug.	0–30	------------------				2	2
Lake Chauekuktuli	Aug.	0–45	1	48	4	4	2	2
Kvichak system								
Iliamna Lake	June-Oct.	0–45	74	3,164	45	45	37	37
Lake Clark	June-Oct.	0–45	---	227	8	8	4	4
PENINSULA SYSTEMS		M.	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*
Alagnak (Branch) system								
Kukaklek Lake	July-Aug.	20	8	17	7	8	4	8
Nonvianuk Lake	July-Aug.	25	9	20	9	9	4	8
Naknek system								
Coville Lake	June-Oct.	25	163	286	149	150	10	14
Grosvenor Lake	June-Oct.	45	198	553	178	178	10	15
Naknek Lake	June-May	35	260	742	254	255	14	19
Brooks Lake	June-May	35	249	675	248	249	15	20
Ugashik system								
Lower Ugashik Lake	Aug.	25	0	18	7	7	5	14
Chignik system								
Chignik Lake	June-Oct.	30	---------		61	54	15	15
Black Lake	June-Oct.	4.5	---------		43	41	11	12
Karluk system								
Karluk Lake	June-Oct.	45	214	557	227	222	15	15

TABLE 3.—*Chemical analyses of water from sockeye salmon nursery lakes of southwestern Alaska, 1961-62*

System and lake	Total dissolved solids	pH	Total alkalinity	Sodium	Potassium	Magnesium	Nitrate nitrogen	Silica	Iron	Manganese	Calcium	Boron	Copper	Strontium	Aluminum	Molybdenum
MAINLAND SYSTEMS	*P.p.m.*		*P.p.m.*	*P.p.m.*	*P.p.m.*	*P.p.m.*	*P.p.m.*	*P.p.m.*	*P.p.m.*	*P.p.m.*	*P.p.m.*	*P.p.m.*	*P.p.m.*	*P.p.m.*	*P.p.m.*	*P.p.m.*
Igushik system																
Amanka Lake	21.5	7.30	10.84	0.55	<0.20	0.75	0.075	4.3	.010	.002	5.10	.007	.0003	.06	.005	.0015
Ualik Lake	17.5	7.13	10.50	.80	.35	.70	.020	2.1	.011	.001	3.95	.011	.0004	.08	.003	.0014
Snake system																
Lake Nunavaugaluk	18.0	7.16	10.42	.55	<.30	.65	.120	2.1	.010	.001	4.90	.007	.0003	.07	.003	<.0001
Wood system																
Lake Aleknagik	30.5	7.15	12.51	.63	.35	.95	.111	2.6	.006	.001	4.95	.008	.0003	.07	.004	.0004
Lake Nerka	20.7	7.14	11.99	.45	.37	.87	.167	2.2	.011	.001	4.68	.015	.0003	.06	.005	.0013
Lake Beverley	24.0	7.21	11.90	.80	<.33	.80	.160	2.8	.008	.001	4.23	.012	.0003	.07	.005	.0004
Lake Kulik	25.3	7.11	12.46	.68	.33	.68	.173	3.0	.009	.001	4.65	.005	.0003	.08	.004	.0015
Little Togiak Lake	35.0	7.29	18.69	.75	.50	1.33	.160	3.3	.006	.001	7.23	.013	.0002	.10	.004	.0006
Nuyakuk (Tikchik) system																
Tikchik Lake	42.0	7.34	22.45	.55	<.70	2.12	.090	5.4	.010	.001	7.70	.010	.0004	.09	.005	trace
Nuyakuk Lake	36.5	7.30	22.99	.40	Trace	1.55	.110	6.4	.007	trace	8.40	.017	.0004	.10	.005	<.0001
Lake Chauekuktuli	50.0	7.29	29.46	.40	Trace	2.60	.135	6.4	.005	trace	11.00	.009	.0004	.10	.003	.0003
Kvichak system																
Iliamna Lake	26.3	7.26	13.96	.83	.60	.83	.058	4.5	.011	<.003	5.11	.022	.0004	.06	.010	.0015
Lake Clark	32.0	7.28	19.59	.80	1.28	1.03	.113	8.6	.026	.001	6.75	.030	.0006	.09	.017	.0028

TABLE 3.—*Chemical analyses of water from sockeye salmon nursery lakes of southwestern Alaska, 1961-62—Continued*

System and lake	Total dissolved solids	pH	Total alkalinity	Sodium	Potassium	Magnesium	Nitrate nitrogen	Silica	Iron	Manganese	Calcium	Boron	Copper	Strontium	Aluminum	Molybdenum
PENINSULA SYSTEMS	*P.p.m.*		*P.p.m.*	*P.p.m.*	*P.p.m.*	*P.p.m.*	*P.p.m.*	*P.p.m.*	*P.p.m.*	*P.p.m.*	*P.p.m.*	*P.p.m.*	*P.p.m.*	*P.p.m.*	*P.p.m.*	*P.p.m.*
Alagnak (Branch) system																
Kukaklek Lake	23.0	7.00	8.88	4.02	1.23	1.15	.018	1.1			3.29					
Nonvianuk Lake	32.5	7.21	10.54	3.25	.90	1.12	.017	4.1	.040	.01	5.33	.003				
Naknek system																
Coville Lake	51.6	7.13	25.28	3.18	.46	1.21	<.014	9.0	.052	.01	7.79	.003				
Grosvenor Lake	53.5	7.24	25.42	2.98	.47	1.89	<.014	7.7	.040	.01	6.90	.003				
Naknek Lake [1]	139.5	7.35	28.54	10.40	1.16	4.16	.087	9.3	.040	.01	18.16	.008				
Iliuk Arm		7.27	28.61													
Brooks Lake	74.8	7.31	26.78	4.30	.95	2.18	.012	10.5	.041	.01	8.88	.004				
Ugashik system																
Lower Ugashik Lake	22.4	7.23	14.57	7.13	.80	1.28	.019	1.4			4.81					
Chignik system																
Chignik Lake	55.9	7.65	21.31	2.35	1.31	3.04	.026	12.9	.024	.002	7.43	.027	.0006	.07	.007	.0011
Black Lake	69.7	7.44	21.53	4.07	1.43	3.04	.014	12.6	.016	.002	10.36	.042	.0009	.12	.010	.0001
Karluk system																
Karluk Lake	42.9	7.25	25.22	3.32	.26	1.47	.036	.4	.042	.01	6.61					

[1] Excluding Iliuk Arm. Iliuk Arm is considered separately because of the large amount of suspended glacial material.

TABLE 4.—*Ranking of sockeye salmon nursery lakes of southwestern Alaska according to total dissolved solids, total alkalinity, and pH, 1961-62*

Lake	System	Total dissolved solids	Total alkalinity	pH
Naknek [1]	Naknek	1	2	3
Brooks	Naknek	2	3	5
Black	Chignik	3	9	2
Chignik	Chignik	4	10	1
Grosvenor	Naknek	5	4	13
Coville	Naknek	6	5	20
Chauekuktuli	Nuyakuk	7	1	8
Karluk	Karluk	8	6	12
Tikchik	Nuyakuk	9	8	4
Nuyakuk	Nuyakuk	10	7	6
Little Togiak	Wood	11	12	8
Nonvianuk	Alagnak	12	20	15
Clark	Kvichak	13	11	10
Aleknagik	Wood	14	15	18
Iliamna	Kvichak	15	14	11
Kulik	Wood	16	16	22
Beverley	Wood	17	18	15
Kukaklek	Alagnak	18	23	23
Lower Ugashik	Ugashik	19	13	14
Amanka	Igushik	20	19	7
Nerka	Wood	21	17	19
Nunavaugaluk	Snake	22	22	17
Ualik	Igushik	23	21	20

[1] Excluding North Arm and Iliuk Arm.

Equivalent Proportions of Sodium, Calcium, and Magnesium

Lakes of the Mainland Systems clearly differ from those of the Peninsula Systems in the proportion (based on number of equivalents per million)[5] of each of the three principal cations —sodium, calcium, and magnesium. To deter-

TABLE 5.—*Mean equivalent proportions of the three major cations—sodium, calcium, and magnesium—in water samples from sockeye salmon lakes of southwestern Alaska, June to September 1961-62*

System and lake	Sodium	Magnesium	Calcium
MAINLAND SYSTEMS	*Percent*	*Percent*	*Percent*
Igushik system			
Amanka Lake	7	18	75
Ualik Lake	12	20	68
Snake system			
Lake Nunavaugaluk	7	17	76
Wood system			
Lake Aleknagik	8	22	70
Lake Nerka	6	22	72
Lake Beverley	11	21	68
Lake Kulik	9	18	73
Little Togiak Lake	6	22	72
Nuyakuk (Tikchik) system			
Tikchik Lake	4	30	66
Nuyakuk Lake	3	23	74
Lake Chauekuktuli	2	27	71
Kvichak system			
Iliamna Lake	10	19	71
Lake Clark	8	19	73
PENINSULA SYSTEMS			
Alagnak (Branch) system			
Kukaklek Lake	40	22	38
Nonvianuk Lake	28	18	54
Naknek system			
Coville Lake	22	16	62
Grosvenor Lake	21	25	54
Naknek Lake	27	20	53
Brooks Lake	23	22	55
Ugashik system			
Lower Ugashik Lake	47	16	37
Chignik system			
Chignik Lake	14	35	51
Black Lake	19	26	55
Karluk system			
Karluk Lake	24	20	56

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[5] Equivalents per million are determined by multiplying the parts per million by the reciprocals of combining weights of the appropriate ions. The combining weight of an ion equals the atomic weight of the ion divided by its ionic charge.

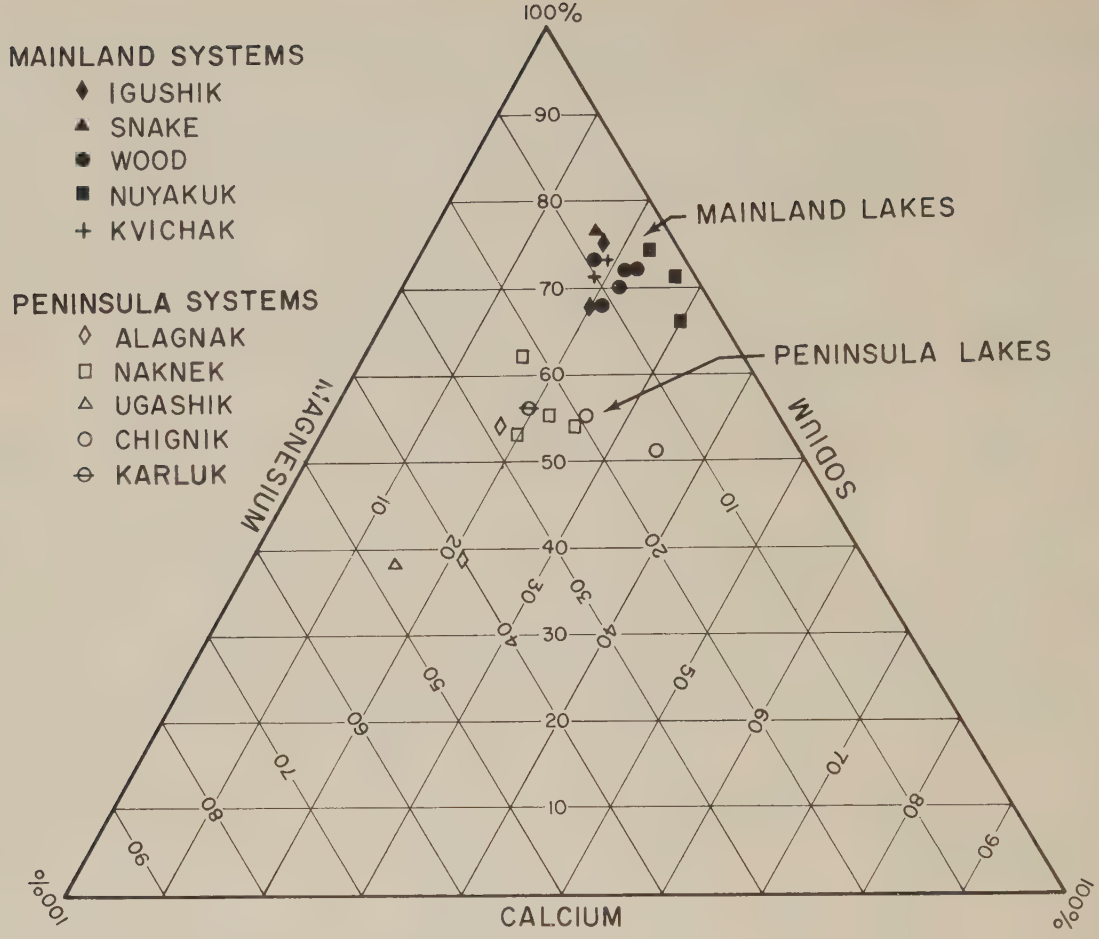

FIGURE 3.—Relative chemical proportions of the three major cations—sodium; calcium, and magnesium—in water samples from sockeye salmon lakes of southwestern Alaska. Each corner of a triangle is assigned a value of 100 percent for one of the cations. If a lake had equal equivalents of each cation, the value for that lake would be plotted in the center of the triangle. As the proportion of a cation increases toward 100 percent for that lake, the point is plotted closer and closer to the corresponding tip of the triangle.

mine these proportions, the concentrations of the three cations in equivalents per million were summed. Then the proportion of the total equivalents contributed by each cation was calculated (table 5). The data are presented graphically in figure 3.

The graphic analysis of the proportionate contribution of the three cations (fig. 3) reveals a similarity among the lakes of a system. Lakes of several systems—Wood, Nuyakuk, Naknek, and Chignik—show this grouping, which suggests that the sources of these elements (terrestrial and marine) influence all lakes within a system similarly. Figure 3 also shows that groups of lakes for systems on the mainland and on the peninsula do not overlap. Lakes of the Mainland Systems have proportionally more equivalents of calcium and less sodium than lakes of the Peninsula Systems. Our last comment on this analysis concerns lakes of the Nuyakuk system. In these waters the absolute concentrations of sodium were comparatively low (table 3), and the proportions of equivalents of sodium in relation to magnesium and calcium are also low (table 5).

Goldman (1960) found low concentrations of magnesium to be limiting to phytoplankton production in Brooks Lake during the summer of 1957. He concluded that magnesium at a low level, in comparison with other cations, was less available to the plankton because of the presence of relatively high quantities of sodium.

Other Nutrients and Trace Elements

We measured all of the dissolved chemicals our facilities permitted because more are either known or suspected to be important in the production of phytoplankton. In addition to those measurements previously discussed, we determined the concentrations of nitrogen, phosphorus, molybdenum, silica, iron, aluminum, boron, and copper.

Because nitrogen is essential for photosynthesis, it is commonly considered as a factor that may limit the production of phytoplankton. Although the ultimate source of nitrogen is the atmosphere, the combined nitrogen in lake water is derived primarily from inflowing waters (Hutchinson, 1957). Goldman (1960) found a nitrate-nitrogen deficiency in Brooks Lake in July and August 1957. In the lakes we studied concentrations of nitrate nitrogen were highest in the Mainland Systems and lowest in the Peninsula Systems (table 3). The lower values in the Peninsula Systems may be due in part to greater use of nitrate nitrogen in the higher production of phytoplankton.[6]

Some investigators have considered phosphorus as a possible limiting factor in the production of phytoplankton in sockeye salmon lakes (Krokhin, 1957; Nelson and Edmondson, 1955; Nelson, 1958; Goldman, 1960). Carcasses of adult salmon are considered an important source of replenishment of phosphorus to sockeye salmon lakes (Krokhin, 1957; Nelson and Edmondson, 1955). The limit of detectability of phosphate in our analysis of water samples was about 0.01 to 0.02 p.p.m. In general, concentrations of phosphorus were below these limits. Since a large part of the total phosphorus is bound in plankton, and phytoplankters are known to store more phosphorus than they need, the rate of phosphorus turnover largely controls the level in solution in water and, hence, determines its availability. Additional measurements and nutritional experiments are needed to establish whether availability of phosphorus is a factor that seriously limits production of phytoplankton in the lakes under study.

From limited nutritional experiments in 1962, Goldman (1964) concluded that low concentrations of molybdenum were limiting the phytoplankton growth in many lakes, including some sockeye salmon lakes of Bristol Bay. We measured molybdenum by colorimetric and spectrographic methods. Concentrations were low in all lakes. Comparison of spectrographic analyses of filtered water and phytoplankton from lakes of the Wood, Kvichak, and Chignik systems in 1964 indicates that molybdenum was generally detectable in water only. This finding indicates that phytoplankters were not concentrating the element. Experiments are needed to clarify the role of molybdenum in the production of phytoplankton.

Silica is necessary for the growth of diatoms and, "the main mechanism of loss of silica from lake waters is its utilization by diatoms. . . ." (Hutchinson, 1957). The peninsula lakes, except for Kukaklek and Lower Ugashik, had the highest concentrations of silica. Lakes of the Wood system had moderate levels; Karluk Lake, although highly productive, had considerably lower concentrations than the other lakes. It is likely that large amounts of silica are bound in the phytoplankton, especially in Karluk Lake, where Hilliard (1959) found that diatoms were the dominant phytoplankters throughout the year.

Some differences were found also between systems in concentrations of the other elements detected regularly in spectrographic analyses of water samples. Lakes in the Chignik system had the highest concentrations of iron, aluminum, boron, and copper; the Kvichak system followed. The concentrations of these elements were lower but fairly uniform in the lakes of the several systems tributary to Nushagak Bay. High concentrations of copper can inhibit growth of phytoplankton, but the concentrations found in this study were low.

Dissolved Oxygen

Concentrations of dissolved oxygen were near saturation whenever lakes were sampled, regardless of depth or season of year; winter samples through the ice were taken only in Naknek and Brooks Lakes.

THERMAL CHARACTERISTICS

Variation in both photosynthetic rates and water temperature during the summer is largely due to variation in solar radiation. Photosynthesis is at the base of primary productivity, and temperature greatly influences the rate of growth of fish; therefore, we measured solar radiation and water temperature in our limnology studies. Many data were collected, but only general comparisons were made among the systems.

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[6] The low rates of productivity in the Ugashik and Alagnak systems are based on only one and two observations, respectively.

Thermal stratification and development of thermoclines are most pronounced in lakes protected from the mixing action of strong and persistent winds. During our study, thermoclines usually were well developed in the upper lakes of the Wood system, which are generally protected from strong winds; they were less well defined in the lower, more exposed lakes. The larger, broadly exposed lakes, such as Iliamna and those of the Naknek system, were generally without thermoclines. Thermoclines were common in the smaller lakes, such as Chignik and Karluk, but were easily destroyed by the strong persistent winds which result from the lakes' exposure to the ocean climate.

PRIMARY PRODUCTIVITY AND STANDING CROP OF PHYTOPLANKTON

The measure of primary productivity used in this study was the rate of carbon fixation by phytoplankton per 4-hour midday incubation period throughout the water column, calculated on the basis of a square meter of the surface and a cubic meter in the euphotic zone. The rate of carbon fixation was determined by the in situ light- and dark-bottle C^{14} technique (method I of Steemann Nielsen, 1952). The measure of the standing crop of phytoplankton was the concentration of chlorophyll *a*. In general, rates of carbon fixation were lower in 1961 than in 1962, but the values for 1962 rather than the averages for 1961-62 are used here to compare lakes because productivity measurements were available for more lakes in 1962. These data along with concurrent measures of the transparency of the water (Secchi disk extinction values) are given in table 6.

The results of our measures of basic productivity are discussed by system.

Mainland Systems

Among lakes of the Mainland Systems, those of the Nuyakuk rank highest in concentrations of total dissolved solids and alkalinity; yet in the single series of observations in two lakes of the system (Tikchik and Chauekuktuli), phytoplankton production and standing crop were low. The average Secchi disk reading of more than 15 m. in Lake Chauekuktuli was the highest in any of the systems—a further indicator of low phytoplankton density; and the rate of carbon fixation per cubic meter had the lowest average for any of the lakes. Deficiencies of trace elements may limit productivity.

The single series of observations of photosynthetic rates in Ualik Lake of the Igushik system and Lake Nunavaugaluk of the Snake system indicated that they were intermediate in the ranking among all systems tested and were similar to those of the Wood system. The standing crops of phytoplankton, however, were lower.

The lakes of the Wood system had carbon fixation rates, chlorophyll *a* concentrations, and Secchi disk readings intermediate in the range of values for all systems. The photosynthetic rate and chlorophyll *a* concentration in Little Togiak Lake were slightly higher than in the other lakes. The differences among lakes in the Wood system were rather small.

Rates of carbon fixation were only slightly lower in lakes of the Kvichak system than in lakes of the Wood system. The photosynthetic rate per cubic meter in the euphotic zone and the chlorophyll *a* concentrations were as high in Lake Clark as in Iliamna Lake, but the total carbon fixed in the water column was less in Lake Clark because of the restricted depth of the euphotic zone (caused by rock flour). The Secchi disk extinction value was only 3.8 m. in Lake Clark, in contrast to 9.8 m. in Iliamna Lake and 8.7 to 12.6 m. in lakes of the Wood system.

Peninsula Systems

Among lakes of the Peninsula Systems, those of the Alagnak system ranked near the bottom in basic productivity and also had low standing crops of phytoplankton.

Lakes within the Naknek system had a wide range in productivity. Shallow Coville Lake is very productive and ranks next to lakes of the Chignik and Karluk systems in primary productivity and standing crop of phytoplankton, whereas deep and clear Brooks Lake is among the least productive systems. The Secchi disk readings in each lake were correspondingly low and high.

In the Ugashik system the primary productivity and standing crop of phytoplankton in Lower Ugashik Lake (the only lake examined) were about as low as in the Alagnak system.

Lakes of the Chignik system had by far the

TABLE 6.—*Primary productivity, chlorophyll* a *concentration, and water transparency for sockeye salmon nursery lakes of southwestern Alaska, 1962*

System and lake	Primary productivity			Chlorophyll *a*		Water transparency	
	Determinations	Mean carbon fixation per 4-hour period per square meter lake surface area	Mean carbon fixation per 4-hour period per cubic meter in euphotic zone	Determinations	Mean concentrations	Samples	Mean Secchi disk reading
MAINLAND SYSTEMS	*Number*	*Mg.*	*Mg.*	*Number*	*Mg./l.*	*Number*	*M.*
Igushik system							
Amanka Lake				1	0.7	2	8.5
Ualik Lake	9	73	2.5	2	.8	3	9.7
Snake system							
Lake Nunavaugaluk	10	66	1.4	1	.6	1	13.0
Wood system							
Lake Aleknagik	240	65	2.0	8	1.3	25	8.7
Lake Nerka	659	58	1.7	22	.9	63	12.6
Lake Beverley	118	71	1.7	8	1.0	11	12.0
Lake Kulik	108	66	1.6	7	.8	11	11.5
Little Togiak Lake	133	73	1.9	6	1.4	14	10.4
Nuyakuk (Tikchik) system							
Tikchik Lake	10	52	1.6	3	.6	3	10.7
Nuyakuk Lake				2	.2	2	10.0
Lake Chauekuktuli	10	54	1.0	3	.5	3	15.3
Kvichak system							
Iliamna Lake	455	54	1.5	165	.8	24	9.8
Lake Clark	41	13	1.6	4	1.1	4	3.8
PENINSULA SYSTEMS							
Alagnak (Branch) system							
Kukaklek Lake	18	22	1.1	4	.6	3	10.2
Nonvianuk Lake	20	24	1.2	4	.5	4	13.2
Naknek system							
Coville Lake	411	99	5.9	80	1.0	72	5.4
Grosvenor Lake	553	61	2.9	85	.7	84	8.4
Naknek Lake [1]	810	59	3.4	86	.9	135	4.4
Iliuk Arm							.9
Brooks Lake	832	47	1.7	73	.5	154	10.8
Ugashik system							
Lower Ugashik Lake	20	41	1.2	4	.8	3	8.5
Chignik system							
Chignik Lake	311	242	13.5	41	15.3	41	1.9
Black Lake	137	121	33.4	26	5.4	28	1.6
Karluk system							
Karluk Lake	606	131	5.9	73	2.1	105	8.6

[1] Excluding Iliuk Arm. Iliuk Arm is considered separately because of the large amount of suspended glacial material.

highest photosynthetic activity and the greatest standing crop of phytoplankton of all lakes studied. Chignik Lake had a high average value for carbon fixed in the water column, but the rate per cubic meter in the euphotic zone was much higher in shallow Black Lake where a high rate of carbon fixation extended to the bottom. Although the low transparency in these two lakes was primarily due to heavy phytoplankton blooms, in Chignik Lake it was partially due to suspended rock flour.

In Karluk Lake, the rate of carbon fixation per cubic meter in the euphotic zone was high but considerably below the rate in the Chignik system. Because of the greater depth of the euphotic zone at Karluk Lake, however, the rate of carbon fixation per square meter of surface was greater than in Black Lake. The Secchi disk readings were 8.6 and 1.6 m., respectively, for Karluk and Black Lakes. The standing crop of phytoplankton in the Karluk system was second only to that of the Chignik system.

PRODUCTIVITY MEASUREMENTS AND SALMON PRODUCTION

Studies of the size of escapements and the growth of progeny indicate that in some systems at least (Wood, Kvichak, and Chignik), the growth of young salmon is slower when population densities are high (see later sections of this paper). This slow growth suggests that the abundance of food in the nursery lake limits production. A primary aim of the limnological studies was to determine if those lakes that usually support high population densities of salmon are basically the more productive. In other words, do they have higher concentrations of dissolved plant nutrients, higher standing crops of phytoplankton, and higher rates of photosynthetic activity?

The only measure of salmon production available for all the systems is the average escapement for recent years. To use this measure we must assume that the average catch-to-escapement ratio is about the same for all systems. Although this ratio can vary somewhat, the escapement levels provide a useful index of salmon production.

The systems are ranked in table 7 according to: (1) the average sockeye salmon escapement per square kilometer of lake surface for 1955-62, (2) primary productivity as indicated by the rate of carbon fixation by photosynthesis per square meter of lake surface and per cubic meter in the euphotic zone, (3) the standing crop of phytoplankton as indicated by the concentration of chlorophyll *a*, and (4) the concentration of total dissolved solids.

The four systems with the higher rates of primary productivity (considering both rate per square meter and rate per cubic meter) produced more adult salmon per square kilometer of lake (Karluk, Chignik, Igushik, and Wood). Among the other systems the correlation between rates of primary productivity and salmon production is not marked. The number of observations was too small in several of the systems to give reliable averages for primary productivity and chlorophyll *a* values; hence, the true rankings of the lake systems may diverge from those given here.

The primary productivity and escapement per unit lake area for the Naknek system are unusual. Although this system does not rank high (no. 6) in rate of carbon fixation in the water column under a square meter of lake area, it does rank high (no. 3) in rate of carbon fixation per cubic meter in the euphotic zone. Furthermore, the escapement per unit lake area is a misleading statistic for this system because two basins, North Arm and Brooks Lake, make up about 32 percent of the area of the system but usually receive only about 5 percent of the escapement. These two basins also have the lowest rates of primary productivity in the system. If North Arm and Brooks Lake were not considered, the Naknek system would rank about no. 5 in terms of escapement and no. 4 or 5 in terms of primary productivity.

TABLE 7.—*Ranking of sockeye salmon nursery lakes of southwestern Alaska according to average escapement density (1955-62), primary productivity, standing crop of phytoplankton, and total dissolved solids (1961-62)*

System	Escapement per square kilometer		Primary productivity (rate of carbon fixation)		Standing crop of phytoplankton (chlorophyll *a* per liter)	Total dissolved solids in p.p.m.
			Per square meter lake surface area	Per cubic meter in euphotic zone		
	Rank	*Number*	*Rank*	*Rank*	*Rank*	*Rank*
Karluk	1	8,350	2	2	2	3
Chignik	2	8,070	1	1	1	2
Igushik	3	4,360	[1]3	[1]4	[1]7	[1]10
Wood	4	2,340	4	5	3	6
Alagnak	5	1,441	10	10	9	5
Ugashik	6	1,338	9	9	6	8
Kvichak	7	1,330	7	7	4	7
Naknek	8	1,122	6	3	5	1
Snake	9	290	[1]5	[1]8	[1]8	[1]9
Nuyakuk	10	280	[1]8	[1]6	[1]10	[1]4

[1] Only a few determinations were made; see tables 2 and 6.

Measurements of the standing crops of phytoplankton (chlorophyll *a* concentrations) and concentrations of total dissolved solids are not clearly related to rate of production of salmon. We cannot expect the standing crop of phytoplankton to be as sensitive a comparative measure of productivity as rates of carbon fixation because of the problems of unknown rates of turnover or utilization of phytoplankton by the zooplankton. Similarly, our measures of total dissolved solids do not give a good estimate of the potential of a system to produce salmon because the phytoplankters need a proper balance of nutrients.

CAPACITY OF SPAWNING GROUNDS

Our purpose in studying the capacity of the spawning grounds was to determine whether the space available is sufficient to produce enough salmon fry to use the nursery areas fully. In considering the amount of spawning ground as a limiting factor, we first present information on the size of past escapements and their characteristics. Next we will estimate potential spawning populations by using estimates of the space available for spawning, estimates of the space requirements of a spawning female, and data on past spawning populations. Finally, we consider the question—is the capacity of the spawning grounds to produce young sockeye salmon less than or greater than the capacity of the lakes to rear them?

MEASURES OF ESCAPEMENT

Statistics on the escapements of sockeye salmon to the major river systems of southwestern Alaska are incomplete before 1955. Between 1900 and 1933, escapement counts were obtained at weirs in a few rivers. Since the late 1930's, rough estimates of escapements have been made by ground and aerial surveys. Weirs were reinstalled in the Chignik and Ugashik Rivers in 1949, in the Naknek River in 1950, and in the Egegik River in 1952. Intensive ground and aerial surveys of spawning grounds in the Wood system were started in 1946. On the Wood River in 1953, FRI first used observation towers to obtain sample counts for estimating escapements of migrating adult salmon. This technique has supplanted weirs in most areas and was extended to the Kvichak River in 1955; the Egegik in 1956; the Naknek, Ugashik, and Alagnak in 1957; the Igushik in 1958; the Nuyakuk in 1959; and the Snake in 1960 (fig. 2). Since 1921, weirs have been used in Karluk River except in 1958 and 1959 when counting towers were used. A weir is still used in the Chignik River.

Size of Escapements

Estimates of the size of escapements to the several river systems in 1955-62 (table 8) provide an index of the relative production of each system. Escapements may vary widely within a system and may be cyclic in some. For instance, in the Kvichak system (which is the only system with clearly defined cycles of abundance of sockeye salmon) the escapement in 1960 was almost 60 times that in 1955. In each of the next three largest systems—Wood, Naknek, and Egegik—the greatest escapements were only six to eight times the smallest. The escapements to Chignik and Karluk Rivers have not varied as much—in the Karluk system the largest was about four times the smallest, and in the Chignik system it was only twice the smallest.

Distribution of Spawners within Systems

Sockeye salmon use four major types of spawning grounds: streams tributary to lakes, rivers between lakes, outlet rivers (trunk streams), and lake beaches. The relative importance of each type varies among systems and from year to year within systems.

TABLE 8.—*Estimates of sockeye salmon escapements to major river systems of southwestern Alaska, 1955-62*

[Thousands of fish]

Year	Igushik	Snake	Wood	Nuyakuk	Kvichak	Alagnak	Naknek	Egegik	Ugashik	Chignik	Karluk
1955	[1] 500	[1] 30	1,383	[1] 16	251	[1] 172	273	269	77	447	386
1956	[1] 400	[1] 4	773	[1] 30	9,443	[1] 784	1,773	1,104	425	748	138
1957	[1] 130	[1] 3	289	[1] 67	2,843	127	635	391	215	509	221
1958	108	[1] 9	960	[1] 196	535	95	278	246	279	325	274
1959	644	[1] 140	2,209	49	680	825	2,232	1,072	219	411	444
1960	495	17	1,016	146	14,630	1,241	828	1,799	2,304	608	349
1961	294	5	461	80	3,706	90	351	702	349	407	297
1962	16	2	874	38	2,581	91	722	1,027	255	483	561
Average	323	26	996	78	4,334	428	886	826	515	492	334

[1] Aerial survey estimates by FRI.

Variation may be considerable in the age composition of sockeye salmon that use the different types of spawning grounds within a given system. The most striking difference is in the number of years the salmon have spent in the ocean. Although most adult sockeye salmon are 2- or 3-ocean fish (i.e., remain in the ocean 2 or 3 years before they return to spawn), the proportion varies among groups of fish occupying specific spawning areas from year to year. Three-ocean fish are larger than 2-ocean and are more susceptible to capture by the gill nets in Bristol Bay.

Natural fluctuations in the relative abundance of various components of a stock, combined with selective effects of the fishery, often lead to poor distribution of the escapement among the spawning grounds. The total escapement may be adequate for a system, but if the distribution of the escapement does not conform to the relative spawning capacities of various grounds, some grounds will be underutilized and others will be overutilized. Various races and age groups of sockeye salmon bound for the many spawning grounds of a system may pass through the fishery at different times. Therefore, the fishery that operates at different intensities through each season could harvest components at different rates—for example, through a combination of net selectivity and closed fishing times. This section examines the evidence bearing on these problems in the sockeye salmon systems of southwestern Alaska.

Igushik system. — The type of spawning grounds used varies greatly from lake to lake

TABLE 9. –*Distribution of spawning sockeye salmon among three types of spawning areas in lakes of the Wood system, 1955-62*

Lake and year	Fish spawning in— Tributary creeks	Lake beaches	Rivers between lakes
	Percent	*Percent*	*Percent*
Aleknagik			
1955	55	0	45
1956	54	2	44
1957	38	2	60
1958	51	5	44
1959	29	5	66
1960	37	5	58
1961	10	2	88
1962	47	6	47
Average	40	3	57
Nerka			
1955	32	55	13
1956	11	43	46
1957	37	49	14
1958	17	74	9
1959	29	5	66
1960	37	49	14
1961	11	43	46
1962	32	55	13
Average	26	47	27
Beverley			
1955	0	95	5
1956	13	85	2
1957	29	70	1
1958	1	95	4
1959	1	95	4
1960	0	94	6
1961	14	76	8
1962	6	85	9
Average	8	87	5
Kulik			
1955	0	53	47
1956	0	49	51
1957	0	16	84
1958	0	90	10
1959	0	61	39
1960	0	63	37
1961	0	51	49
1962	0	88	12
Average	0	59	41

in the Igushik system. Most sockeye salmon spawn on the beaches at Lake Ualik and in the streams at Lake Amanka.

Wood system. — The distribution of adult sockeye salmon among the three types of spawning grounds in the Wood system differs markedly from lake to lake, but each lake has a characteristic distribution (table 9). For example, tributary creeks and the rivers between lakes receive the greatest part of the spawners in Lake Aleknagik (over 90 percent from 1955 to 1962), whereas in Lake Beverley almost 90 percent of the spawners use the lake beaches. The spawners in Lake Nerka are usually distributed about equally among the three types of spawning grounds. The year-to-year changes in distribution of the spawners in the system as a whole are largely the result of changes in the relative escapement to each lake.

Most sockeye salmon entering the Nushagak fishing district are bound for lakes of the Wood system. Tagging results in 1961 indicated that spawners bound for the different lakes of the Wood system may have passed through the fishery at different times. Overlap was considerable, however, and the same pattern of entry may not occur every year. Time of passage to the two major river spawning grounds, Agulowak and Agulukpak Rivers, was average for the system.

Although the percentages of 2-ocean and 3-ocean sockeye salmon in the run vary annually with year class strength and other undetermined factors, consistent differences in age composition tend to prevail among spawning groups. For instance, in 1960-62, samples of spawning sockeye salmon from Agulowak and Agulukpak Rivers consistently had a higher proportion of 3-ocean fish than samples from other areas of the system (table 10).

TABLE 10.—*Proportions of 3-ocean sockeye salmon in escapements from areas of the Wood system, 1960-62*

Year and sex	Agulowak River	Agulukpak River	Average for remaining areas
	Percent	*Percent*	*Percent*
1960			
Male	80	49	16
Female	84	66	18
1961			
Male	99	92	60
Female	100	96	69
1962			
Male	42	40	8
Female	76	64	7
Average	80	68	30

Nuyakuk system. — The type of spawning grounds used also varies greatly among the lakes of the Nuyakuk system. Sockeye salmon in Lake Chauekuktuli spawn almost exclusively on beaches; in Tikchik Lake they spawn only in rivers and creeks. The escapement to the Nuyakuk system has a consistently higher proportion of 3-ocean fish than that to the Wood system.[7]

Kvichak system. — Sockeye salmon of the Kvichak system spawn in streams tributary to lakes, rivers between lakes, beaches of Iliamna Lake, and spring-fed ponds, which are usually located at the heads of small tributaries. They spawn also in the tributaries to, and on beaches of, small lakes. Some of the fry from these small lakes migrate to nursery areas in Iliamna Lake or Lake Clark.

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[7] Burgner, R. L. 1965. Age composition of Nushagak sockeye runs by river system. Univ. Wash., Fish. Res. Inst., Circ. 234, 14 pp.

The distribution of the escapements to large streams, lake beaches, and all other spawning grounds of the Kvichak system in 1959-62 is shown in table 11. When the escapement was extremely large in 1960, the beaches of Iliamna Lake received a larger proportion of the total escapement and the large streams received a smaller proportion than in years when the escapements were smaller. The importance of the other spawning grounds remained nearly constant from 1959 to 1962.

TABLE 11.—*Distribution of sockeye salmon escapements in spawning grounds of the Kvichak system, 1959-62*

Year	Fish in escapement	Fish spawning in— Large streams	Beaches of Iliamna Lake	All others
	Millions	*Percent*	*Percent*	*Percent*
1959	0.7	57.8	25.4	16.8
1960	14.6	26.9	50.0	23.1
1961	3.7	55.0	33.8	11.2
1962	2.6	64.7	19.7	15.6

Escapements to large streams have varied by a factor of 10, whereas those to the system varied by 20 and those to the lake beaches by about 50. Thus, the cyclic nature of the production of sockeye salmon in the Kvichak system could be reinforced or perhaps caused by the cyclic nature of the production from the beaches alone.

We found marked contrasts in age characteristics — both ocean and fresh-water — among spawning groups in the Kvichak system in 1962. Stream spawning groups (except those of the Copper River) had a significantly lower proportion of 3-ocean fish than beach spawning groups.[8] Differences also existed in the average fresh-water age of various spawning groups in the Kvichak system in 1956-58 (Koo and Smith, 1960).

Smith (1964) found little or no difference in the time the various spawning groups entered the Kvichak system in 1957, 1958, and 1959. Adult sockeye salmon were tagged as they entered Iliamna Lake, and the tagged fish were recovered on the spawning grounds. The migration into the lake lasted about 4 weeks. Fish tagged in any one of these weeks were recovered in about the same proportion in large and small streams, on lake beaches, and in spring-fed ponds, regardless of whether spawning in these places occurred early or late in the season.

Naknek system. — The principal spawning grounds of the Naknek system are: (1) Brooks and Grosvenor Rivers (rivers between lakes); (2) American and Hardscrabble Creeks (tributary streams); (3) Naknek River (outlet or trunk river); and (4) beaches of Grosvenor Lake. Some sockeye salmon also spawn on beaches in Iliuk Arm and South Bay of Naknek Lake. The proportions of sockeye salmon that spawn on the several major spawning grounds change markedly from year to year. In some years a single major ground may receive more than 60 percent of the escapement to the system and in other years the same ground may receive less than 10 percent.

Each of the major groups of spawning sockeye salmon in the Naknek system in 1962 was characterized by different proportions of combinations of fresh-water and ocean ages (Straty, 1966). Most major spawning grounds contained a smaller proportion of adults that migrated seaward as age II smolts than did the total escapement to the Naknek River. This anomaly suggests the existence of spawning groups as yet undetected.

Tagging in the Naknek River in 1961 and 1962 demonstrated that all major spawning areas within the system received fish from all parts of the run about in proportion to the sizes of the spawning groups (Straty, 1966). Some slight indication appeared, however, that Brooks Lake and Brooks River received more of the earlier fish than the other areas.

Chignik system. — Sockeye salmon in runs to the Chignik system are predominantly 3-ocean fish. The greatest contrast in age composition in this system is in the time the young live in fresh water: most of the smolts migrate at age I from Black Lake and at age II from Chignik Lake.

Tagging and studies of scales have established that adults returning to Chignik and Black Lakes pass through the fishery at different times (Narver, 1963). The early run (in June) has primarily sockeye salmon bound for Black Lake, and the late run (in July and August) has primarily fish bound for Chignik Lake.

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[8] Kim, Wan Soo, and Robert L. Demory. 1963. Kvichak salmon studies, 1962 spawning ground studies. Univ. Wash., Fish. Res. Inst., Circ. 195, 26 pp.

Karluk system. — The distribution of sockeye salmon on the spawning grounds in the Karluk system has been well documented from data collected on weekly surveys carried out on foot each summer in 1947-62. Salmon that enter the system during May, June, and July tend to occupy all tributaries; those entering during August and September tend to occupy only the large tributaries at the south end of the lake, the lake beaches, and the outlet river.[9]

Sockeye salmon in Karluk Lake have a marked temporal as well as spatial segregation by age group (Rounsefell, 1958; also see footnote 9). In general, salmon that spend the longest time in the ocean (3 years or more) return early in the spawning season and those that spend the least time at sea return late. Since late spawners tend to occupy the large terminal streams, lake beaches, and the upper end of Karluk River, these areas usually receive a disproportionately large number of smaller 2-ocean fish.

The Chignik and Karluk systems contrast sharply with the systems tributary to Bristol Bay in having temporal segregation of spawning units in the trunk river. The absence of marked segregation in Bristol Bay systems may be the result of the short duration of these runs. In general, the Bristol Bay runs last about 4 weeks, and more than 50 percent of each run enters the fishing areas and trunk streams during a few days in early July. In the Chignik and Karluk systems the escapements enter the trunk stream over a 2- to 4-month period.

POTENTIAL SPAWNING POPULATION

The physical capacity of the rivers or beaches to contain adult sockeye salmon imposes a limit on the number of fish that could spawn in each system. It was obvious, however, that a large portion of most of the rivers and beaches was in fact unsuitable for spawning and that the amount of space required for a pair of salmon to spawn varied among different types of spawning grounds. Therefore, to estimate the capacity of each river or beach in terms of numbers of females we determined the area of potential spawning ground and divided this figure by the estimated area required per female.

Estimates of Area of Potential Spawning Grounds

The amount of potential spawning ground for streams and for lake beaches was measured to determine if the area of suitable spawning grounds might limit salmon production in any of the river systems. The data obtained are first approximations because complete and accurate surveys of all spawning grounds could not be completed in 2 years. Estimates of suitable potential spawning area were made for the Wood, Kvichak, Naknek, and Karluk systems (table 12).

During the 2-year study period, catalogs of spawning grounds, which contain descriptions of the physical characteristics and estimates of the area of the potential or utilized spawning grounds and estimates of annual escapements

TABLE 12.—*Estimates of surface area of potential sockeye salmon spawning grounds in streams and lake beaches of Wood, Kvichak, Naknek, and Karluk systems*

System and lake	Streams	Lake beaches	Total
	Hectares	*Hectares*	*Hectares*
Wood system			
Lake Aleknagik	134.6	[1] 86.2	220.8
Lake Nerka	40.9	[1] 1,437.0	1,477.9
Lake Beverley	47.0	[1] 862.6	909.6
Lake Kulik	11.7	[1] 337.9	349.6
Little Togiak Lake	7.2	[1] 108.9	116.1
Total	241.4	2,832.6	3,074.0
Kvichak system			
Iliamna Lake	649.6	[2] 33.0	682.6
Gibraltar Lake	23.0	28.8	51.9
Lake Clark	167.1	49.7	216.8
Total	839.7	111.5	951.3
Naknek system			
Coville Lake	111.0	(3)	------------
Grosvenor Lake	29.6	(3)	------------
Naknek Lake [4]	188.3	(3)	------------
North Arm	7.5	(3)	------------
Brooks Lake	18.0	(3)	------------
Total	354.4	(3)	------------
Karluk system			
Karluk Lake	33.7	[5] 1.2	34.9

[1] Estimates based on gravel types only.

[2] Minimum estimate based on incomplete information.

[3] No estimate made.

[4] Excludes North Arm; North Arm is considered separately because it constitutes a rearing area for juvenile salmon discrete from the rest of Naknek Lake.

[5] Only the beach spawning areas of Thumb and O'Malley Lakes are included here.

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[9] Owen, John B., Charles Y. Conkle, and Robert F. Raleigh. 1962. Factors possibly affecting production of sockeye salmon in Karluk River, Alaska. Bur. Commer. Fish. Biol. Lab., Auke Bay, Alaska. [Manuscript, 57 pp.]

by stream, were completed for the Kvichak system (Demory, Orrell, and Heinle, 1964) and the Wood system (Marriott, 1964). A catalog for the Naknek system is being prepared.

The amount of potential spawning grounds for streams was estimated as follows: (1) The stream was divided into sections from the mouth to the upper limit of possible spawning, i.e., to the source or to obstructions to the passage of fish, e.g., falls and beaver dams. (2) The total area of each section was determined. (3) The percentage of each section not usable for spawning was estimated on the basis of bottom composition, gradient, and water velocity. Bottom types defined as not usable included silt, bedrock, and large rock. Pools and torrential water were considered unsuitable for spawning. (4) The amount of potential spawning grounds in each section was estimated by subtracting the area unsuitable for spawning from the total area. Spring-fed ponds were treated as streams.

Wood system.—The estimates of the amount of potential spawning grounds in streams of the Wood system (table 12) apply only to streams in which spawning had been observed.

Size of the gravel and depth of the water were used in the lakes of the Wood system as criteria in estimating the area of beach suitable for spawning. The area of lake surface from the shore to 10-m. depth contours (over bottom judged by field observations to be suitable for spawning) was measured on bathymetric maps. Because other factors, such as upwelling ground water, also appear to be important in beach spawning, the estimates based only on size of the gravel and depth of the water exceed the amount of potential beach spawning grounds.

Kvichak system.—The estimates of the amount of spawning grounds in the Kvichak system are minimal. For stream spawning, estimates were made only for streams in which spawning had been seen. For beach spawning in Iliamna Lake, estimates were made only for beaches on which a small escapement of sockeye salmon had spawned (1961). Beaches in the following areas were not examined: Flat Island, Southeast Beaches, Tommy Beach, Lonesome Bay, and Finger Beach.

Observations in Iliamna Lake during the spawning of a large escapement (1960) indicated that beach spawning was much more extensive than was formerly thought, particularly around islands, where it extended to depths of 30 m.

Naknek system. — Estimates of the amount of potential sockeye salmon spawning grounds are available for all streams in the Naknek system, even those in which spawning has never been seen. The reliability of the estimates varies from stream to stream, and the estimates will be modified as more information is obtained.

Sockeye salmon spawn on beaches in Grosvenor Lake and in a lesser amount in other lakes in the Naknek system, but the extent of these spawning grounds has not been estimated.

Karluk system. — Data on the amount of spawning grounds in the Karluk system are from Owen et al. (footnote 9) and are for grounds on which sockeye salmon are known to spawn.

Estimates of Space Requirements of Spawning Females

A spawning female sockeye salmon requires a certain minimum area of gravel bed in which to deposit her eggs. Eggs are buried in about five pockets in an area of disturbed gravel known as the redd. During construction of the redd and spawning and postspawning activities, both the female and male defend a certain territory surrounding the redd.

Wood and Kvichak systems. — Estimates of the minimal space requirements for spawning females in the Wood and Kvichak systems were based on the egg-carrying capacity of the gravel independent of observed spawning density.

Three principal sources of loss of eggs were considered: (1) increased retention of the eggs by the female because of increased density of spawners, (2) dislodgment of eggs from the redds because of repeated excavations of the same gravel by subsequent females (superimposition), and (3) increased egg mortality because of crowding of eggs in the gravel. Data from the Wood and Kvichak systems indicate that as spawning density increases, superimposition of redds limits survival of the eggs. We estimated egg loss from superimposition to be less than 10 percent with a spawning density of one female per 2 m.^{2} This density is low enough to avoid significant egg loss by increased retention or crowding of eggs in the gravel. Calculation of the capacity of streams in the Wood and Kvichak systems to support spawning sockeye salmon is based, therefore, on a density of one female per 2 m.^{2}

Naknek and Karluk systems. — General observations had indicated that the space requirements for spawning female sockeye salmon vary with differences in quality of the gravel and size and stage of the stream and that the space used by a spawning female is elastic — large when escapements are low and small when they are high. We estimated, therefore, the space requirement for a spawning female from maximum observed densities of spawners in measured sections of streams in the Naknek system. Average densities for entire streams were used in the Karluk system.

Our studies confirmed the earlier general observations that space requirements vary among different kinds of streams. For example, in the large and relatively deep rivers between lakes and the terminal rivers in the Naknek system, the space requirements are between 4 and 9 $m.^2$ per female. In the smaller streams the requirements are much less — 2 to 3 $m.^2$ In the open-water beach areas the requirements are probably similar to or perhaps larger than those in the large rivers. In the shallow torrential lateral streams in the Karluk system, space requirements were often substantially less than 2 $m.^2$ (table 13), but 2 $m.^2$ would appear typical for the system as a whole on the basis of stream survey data from many areas (Richard Gard, personal communication).

Our calculations of the potential capacity of the streams in the Naknek and Karluk systems to support spawning sockeye salmon are based on the estimate of maximum density for each type of stream.

Estimates of Potential Spawning Capacity by System

The potential capacity for the streams in each system to support spawning adults was based on the amount of potential spawning grounds and the space required per spawning female. The potential spawning capacities of the beach areas were estimated from escapement surveys and various other data.

Wood system. — The potential spawning area of rivers and streams (including connected ponds) of the Wood system was estimated to be 241.4 hectares (table 12), and the area required per spawning female was estimated to be 2 $m.^2$ By dividing the spawning area by the area required per female and assuming a 1:1 sex ratio, we calculate that the maximum spawning population in streams in the Wood system is 2,414,000 sockeye salmon.

The maximum numbers of sockeye salmon observed on each spawning ground in 1946-62 were summed by lake for stream spawning and for beach spawning. Since only about 43 percent of the fish that enter the system (estimated by counts from towers) are seen during spawning surveys, the summed maxima have been increased to produce the estimate of the maximum populations for streams and for lake beaches (table 14).

Maximum populations and the estimated potential capacity of the spawning grounds in streams are thought to be in reasonable agreement, because use of the spawning grounds is highly variable and some of the larger streams

TABLE 13.—*Estimated numbers of potential redd sites in various types of spawning grounds of the Naknek and Karluk systems*

System and type of spawning ground	Area of potential spawning ground	Area required per female	Redd sites
	Hectares	*$M.^2$*	*Number*
Naknek system			
Terminal streams	124.9	4.1	302,000
Small lateral streams	12.3	2.6	47,000
Large lateral streams	62.7	7.6	83,000
Rivers between lakes	7.2	[1] 8.8	8,000
Outlet river	147.3	8.0	184,000
Lake beaches			(2)
Total	354.4	----	624,000
Karluk system			
Terminal streams	1.67	2	8,000
Lateral streams	6.71	2	34,000
Lake beaches	1.25	2	6,000
Outlet river	25.28	2	126,000
Total	34.91	----	174,000

[1] Does not take into consideration successive waves of spawners.

[2] An estimate of 20,000 redd sites is based on number of fish seen using the beaches of Grosvenor Lake. Other beach spawning areas exist.

TABLE 14.—*Estimated maximum populations of adult sockeye salmon in streams and lake beaches of Wood system in any year between 1946 and 1962*

Lake	Fish in—		
	Streams	Lake beaches	Total
	Number	*Number*	*Number*
Aleknagik	622,000	15,000	637,000
Nerka	929,000	392,000	1,321,000
Beverley	98,000	487,000	585,000
Kulik	94,000	144,000	238,000
Little Togiak	16,000	47,000	63,000
Total	1,759,000	1,085,000	2,844,000

have very small populations. Because the maximum number of spawners estimated on beaches is less than the maximum estimated in streams (table 14), the spawning ground potential of the beaches is probably not in excess of that of the streams.

The largest escapement of sockeye salmon to the Wood system since counting from towers began in 1953 was 2,209,000 in 1959 (table 8). Although some spawning grounds were overcrowded in 1959, as evidenced by a large mortality of eggs, most were greatly underutilized. Escapements in 1955-62 varied between 289,000 and 2,209,000 sockeye salmon. Thus, the potential capacity of the spawning grounds in the Wood system greatly exceeds the normal escapements.

Kvichak system. — The area of potential spawning grounds in rivers, streams, and ponds in the Kvichak system was estimated to be 839.7 hectares (table 12), and the space required per spawning female was estimated to be 2 m.^{2} A capacity of 4,199,500 spawning females is calculated from these data; on the basis of 1:1 sex ratio, the potential capacity of the nonlake spawning grounds in the Kvichak system is about 8,399,000 spawners.

We do not have enough data to make a direct estimate of the area of the potential beach spawning grounds in the Kvichak system, but we can estimate it indirectly. The area used by 3,706,000 spawners in 1961 on 16 of 21 recognized spawning beaches was 111.5 hectares (table 12). The area used by the 14,630,000 spawners of 1960 would have been 435 hectares if we assume a constant relation between numbers of spawners and area used (the ratio of spawners in 1961 and 1960 was 1:3.9). Because only 75 percent of the beaches known to be used have been surveyed, the estimate of 435 hectares is further expanded by 4/3, to give 579.9 hectares of beach actually used in 1960. Because only beach areas used for spawning have been considered and the average use of potential spawning grounds in the streams has been 48 percent, the amount of potential beach spawning grounds was calculated by assuming the same rate. This computation gives an estimate of 1,208 hectares of potential beach spawning grounds with a capacity of 12,080,000 spawners.

On the basis of the above information, we postulate a potential spawning population of about 20,500,000 sockeye salmon for the Kvichak system. This figure is greater than the maximum observed escapement through 1962. Escapements since 1955 have varied between 251,000 and 14,630,000 (table 8).[10]

Naknek system. — The amount of potential spawning ground in the Naknek system, the space required per female, and the capacity of the spawning ground were calculated for each of several types of streams. We made estimates of the total potential of the beach spawning grounds.

The total number of potential redd sites — calculated from estimates of the amount of spawning ground available and the size of redd sites—is 624,000 for the streams of the Naknek system (table 13). An estimate of 20,000 redd sites for the beach spawning grounds of Grosvenor Lake is based on past spawning ground surveys. Other beach spawning grounds exist, but their capacity is unknown.

Since estimates of the size of redd sites were based on observations of spawning density on single days, the effect of spawning in waves or surges must be considered. Three waves of fish commonly enter the Brooks River (Hartman, Merrell, and Painter, 1964), which is the major interconnecting stream that produces sockeye salmon. The number of redd sites in the interconnecting streams has been expanded, therefore, by a factor of 3 to produce a more realistic estimate of the capacity of these areas to receive spawning salmon.

If all of these factors are considered and a 1:1 sex ratio is assumed, the estimated spawning capacity of the Naknek system is about 670,000 females, or 1,340,000 fish of both sexes. Escapements in recent years varied between 273,000 and 2,232,000 salmon (table 8). Escapements exceeded 1,260,000 twice in the 14 years from 1949 to 1962.

Karluk system. — Estimates of the size of a redd site for several tributaries in the Karluk system are about 2 m.^{2}, and because estimates are not available for other areas, 2 m.^{2} is used for all. The estimated number of redd sites for streams and lake beaches is 174,000 (table 13), and (assuming a 1:1 sex ratio) the capacity is

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[10] The escapement in 1965 was 24.3 million. Some of the spawning grounds had few adult fish; others were so densely occupied that superimposition of redds and retention of eggs caused a great loss of eggs. On most spawning grounds, however, density appeared to be optimal and confirmed the figure given above.

348,000 adults. This estimate is only approximate — the situation in the Karluk system is complicated by the occurrence of successive waves of spawners in most streams and incomplete information on the amount of potential spawning ground, especially on lake beaches. Escapements to Karluk neared or exceeded 1 million fish for many years during the early 1900's.

SPAWNING AREA AS THE LIMITING FACTOR IN PRODUCTION

An excessive density of spawners may cause increased retention of eggs, loss of eggs because of dislodgment from gravel during spawning, and increased mortality of eggs because of crowding of eggs in the gravel. We do not know the relation between these variables and density of spawners.

With the possible exception of the Karluk system, the tentative data on potential spawning areas indicate that the major lake systems could accommodate spawning populations considerably in excess of average present-day escapements. Full use of potential spawning grounds would, however, require a distribution of spawners strictly in proportion to the capacity of each ground. Such a distribution has never been observed.

CAPACITY OF REARING AREAS

Young sockeye salmon usually emerge from the spawning gravels in the spring to begin their stay in the rearing areas of the lakes. Here they remain 1 or 2 years (occasionally 3, as at Karluk) before they migrate seaward in May, June, and July as smolts. The abundance and growth of juvenile sockeye salmon and the age and size of smolts produced in each system were determined and were examined in relation to several physical and biological factors of the rearing areas: (1) number of spawning sockeye salmon per unit of rearing area; (2) relative numbers of other fish species in each system, both possible competitors and predators; (3) movement of presmolt sockeye salmon within and between lakes of a system; (4) basic biological productivity of the waters; and (5) innate characteristics of the various stocks of sockeye salmon.

Because long-term observations were not available for most individual systems, the carrying capacity of each system was judged by means of comparisons among the several systems of the biological and physical characteristics of the rearing areas.

RELATION BETWEEN NUMBERS OF SPAWNERS AND SIZE OF REARING AREAS

In the systems of southwestern Alaska the capacity of the rearing areas to support sockeye salmon is, in general, reflected in the number of adults returning to each system. The most extensive data on the comparative numbers of fish in the returns are found in the escapement records; the escapement is also generally a good indicator of the magnitude of the total return. Because the size of the lakes and systems considered varies widely, the escapements and other measures of productivity are frequently expressed as numbers per square kilometer of lake area. Table 15 gives the average number of adults in the escapements in 1955-62, the area of the lakes, and the numbers of spawners per square kilometer of lake for the major systems in southwestern Alaska.

The systems fall into four general levels of escapement per unit area (table 15): (1) escapements that averaged about 8,000 spawners per square kilometer (Karluk and Chignik); (2) escapements of about 2,300 to 4,400 spawners per square kilometer (Igushik and Wood); (3) escapements between 1,100 and 1,500 spawners per square kilometer (Kvichak, Alagnak, Naknek, and Ugashik); and (4) escapements less than 800 spawners per square kilometer (Egegik, Snake, and Nuyakuk).

For some systems data are available for examining variation in productivity between lakes (in terms of numbers of adults in the escapements to individual lakes) and between years within lakes.

TABLE 15.—*Average sockeye salmon escapements, area of lakes, and spawners per square kilometer of lake by system in southwestern Alaska, 1955-62*

System	Fish in escapement	Lake area	Spawners per square kilometer
	Thousands	*Km.^{2}*	*Number*
Igushik	323	74	4,360
Snake	26	89	290
Wood	996	425	2,340
Nuyakuk (Tikchik)	78	279	280
Kvichak	4,334	2,889	1,500
Alagnak (Branch)	428	297	1,441
Naknek	886	790	1,122
Egegik	826	1,132	730
Ugashik	515	385	1,335
Chignik	492	61	8,070
Karluk	334	40	8,350

Igushik System

In the Igushik system, in 1955-62 the number of spawners per square kilometer of lake in Ualik Lake was only slightly larger than in Amanka Lake if we assign the adults spawning in the interconnecting river and its branch (Ongoke River) to Amanka Lake.

Snake System

Nunavaugaluk Lake is the only lake in the Snake system that produces significant numbers of salmon.

Wood System

The average numbers of spawners per square kilometer in each of the four main lakes of the Wood system in 1955-62 were: Aleknagik, 2,090; Nerka, 2,430; Beverley, 2,490; and Kulik, 2,040. Little Togiak Lake, tributary to Lake Nerka, had a slightly higher density of spawners than the main lakes.

Nuyakuk System

The low average number of spawners per unit lake area in the Nuyakuk system (table 15) is largely due to the low densities in Nuyakuk Lake, the largest lake in the system, where the figure was only 50 spawners per square kilometer from 1959 through 1962.

Kvichak System

The Kvichak is the only major sockeye salmon system in Bristol Bay that has a pronounced cyclic variation in number of adults in the escapement. The effects of this cycle overshadow problems of distribution of the spawners within each year. Over the years 1955-63, the number of spawners per square kilometer of lake varied from 84 — among the lowest numbers observed in Bristol Bay — to 4,890 (table 16). Peak years modify the reproductive potential in subsequent off years. This problem is discussed later.

Naknek System

Many nursery areas of the Naknek system receive juvenile sockeye salmon from upsystem areas; that is, from other than adjacent beaches and tributary streams. Coville Lake represents about 3 percent of the rearing area of the Naknek system but has received as much as 65 percent of the escapement in a given year. This lake is at the upper end of the system, and many of the juvenile sockeye salmon that originate in its tributaries spend some growing time in downsystem lakes. North Arm basin and Brooks Lake make up about 35 percent of the area of the system but receive less than 10 percent of the escapement, and they do not receive fry produced in other areas. The distribution of escapement and subsequently the distribution of the juveniles are considered later.

TABLE 16.—*Numbers of sockeye salmon in escapements and spawners per square kilometer of lake, Kvichak system, 1955-63*

Year	Fish in escapement	Spawners per square kilometer
	Thousands	*Number*
1955	251	84
1956	9,443	3,156
1957	2,843	950
1958	535	179
1959	680	227
1960	14,630	4,890
1961	3,706	1,239
1962	2,581	863
1963	339	113

Chignik System

Chignik Lake had the greatest average concentration of spawners in the Chignik system — about 14,000 per square kilometer of lake in 1956-62. The average for Black Lake during the same period was slightly more than 4,600, about the same as for the Igushik lakes.

Karluk System

Recently emerged fry behave in such a way in the Karluk system that the total escapement is assignable to Karluk Lake for consideration of rearing areas. The progeny of spawners that use the outlet (Karluk River) move upstream into the lake, and progeny of spawners from areas above O'Malley and Thumb Lakes move down into Karluk Lake early in their first summer of life.

SPECIES OF FISH IN THE LAKES

Knowledge of the abundance of species of fish associated with juvenile sockeye salmon in the lakes is essential to understand the factors that may affect the survival and growth of sockeye salmon. Differences in behavior and the distribution of the habitat of the many species required the use of several types of collecting gear: tow nets, beach seines, trap nets, gill nets, and bottom and midwater trawls.

Although as many as 25 species of fish were found in a system, the abundance of most was low. Species of salmon other than sockeye were not sufficiently abundant to compete seriously for rearing area. Juvenile sockeye salmon and one other species of fish constituted 75 to 95 percent of the catches.

Of the species that may be competitors with juvenile sockeye salmon, the threespine stickleback *(Gasterosteus aculeatus)* is most important in the Igushik, Snake, Wood, Kvichak, Nuyakuk, Chignik, and Karluk systems and part of the Naknek system. In other parts of the Naknek system the ninespine stickleback *(Pungitius pungitius)*, pond smelt *(Hypomesus olidus)*, or pygmy whitefish *(Prosopium coulteri)* seem to be of greatest significance. Species of fish in most systems that have varying degrees of importance as predators on juvenile sockeye salmon include Arctic char *(Salvelinus alpinus)*, lake trout *(S. namaycush)*, northern pike *(Esox lucius)*, juvenile coho salmon *(O. kisutch)*, and Dolly Varden *(S. malma)*.

The data on the species in the other systems of southwestern Alaska are too few to permit generalizations.

MIGRATION OF PRESMOLT SOCKEYE SALMON

To study the relation between density of parent spawners (numbers per unit lake area), growth and abundance of progeny, and capacity of the rearing areas, we had to know how long the young sockeye salmon remain in the lake that they first enter as fry. Fyke nets were fished, therefore, in some interconnecting rivers during the summer to detect possible migrations from various lakes. Changes in length frequencies of juveniles and their abundance in tow net catches supplied indirect information on their movements.

Wood System

Catches of fyke nets fished in the connecting rivers of the Wood system indicated no appreciable migration of young sockeye salmon during the summer between Little Togiak Lake and Lake Nerka in 1961 or between Lake Nerka and Lake Aleknagik in 1962.[11] Two other kinds of observations in the Wood system support the conclusion that these fish do not migrate during the summer: (1) the abundance of young-of-the-year in tow net catches after mid-August is generally proportional to the number of parent spawners for each lake (the density of spawners varies widely between lakes within years); and (2) the growth of young-of-the-year is often reduced in lakes that had high densities of spawners the previous fall. We, therefore, assumed that in the main lakes of the Wood system, juvenile sockeye salmon remain within their lake of origin at least during their first growing season.

Kvichak System

Most of the sockeye salmon in the escapement to the Kvichak system spawn in tributaries or on beaches in Iliamna Lake. The only possible significant presmolt interlake migration would be from Lake Clark to Iliamna Lake, and we have no indication that this movement occurs. We investigated this problem directly only at the time of normal smolt migrations in 1959, 1962, and 1963 when we found that the juveniles leaving Lake Clark are mostly age II.[12] Because no age III smolts have been captured at the outlet of Iliamna Lake and no adults with three freshwater annuli have been captured in the system, we assume that the age II juveniles migrating in June from Lake Clark are smolts that pass directly to the outlet of Iliamna Lake. As indicated elsewhere in this paper, the abundance of spawners within Iliamna Lake is greatest in the east end. This concentration produces a greater abundance of fry in that area. Entire age groups move in the lake toward the outlet in the west end, however; this movement is comparable to interlake migrations in other systems.

Naknek System

Interlake migrations of presmolt (age 0 and age I) sockeye salmon are known in the Naknek system.[13] In one movement fish left an area of high density of juveniles to enter areas of low densities (Coville Lake to downlake areas), and in another the migration was from a low- to a high-density area (Brooks Lake to Naknek

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[11] Burgner, R. L., and J. M. Green. 1963. Study of interlake migration of red salmon fry, Agulowak River. Univ. Wash., Fish. Res. Inst., Circ. 182, 13 pp.

[12] Orrell, R. F. 1963. Abundance and age of Lake Clark red salmon smolts, 1962. Univ. Wash. Fish. Res. Inst., Circ. 186, 13 pp.

[13] Ellis, Robert J. 1963. The abundance and distribution of juvenile red salmon and associated species in lakes of the Naknek River system and Karluk Lake. Bur. Commer. Fish. Biol. Lab., Auke Bay, Alaska. [Manuscript, 80 pp.]

Lake). The interlake and interbasin migrations of presmolt fish in the Naknek system caused large numbers of fish to accumulate in downsystem lake areas, which have comparatively limited spawning grounds. Fyke net catches from Coville, Grosvenor, and Brooks Rivers and tow net catches from the lakes indicate that Naknek Lake, except for the relatively isolated North Arm basin, serves as a rearing area for fish originating in other lakes.

Chignik System

Interlake migration of age 0 sockeye salmon from Black Lake to Chignik Lake was detected by fishing fyke nets in Black River in 1961 and 1962. Scales of age 0 and age I salmon from Chignik Lake indicate that some Black Lake progeny use Chignik Lake as a rearing area, but scales from spawning populations in Black Lake indicate that most fry remain in Black Lake to age I and then migrate directly to the ocean (Narver, 1963). Extensive sampling of Chignik Lagoon with tow nets and seines in 1962 and 1963 revealed that some of the progeny of spawners of Chignik Lake migrate into Chignik Lagoon soon after they emerge from the gravel and use the lagoon as a rearing area.

Karluk System

Interlake movements of presmolt sockeye salmon have not been investigated in the Karluk system. Because Karluk Lake is the only rearing area of significant size, these movements could not be important.

ABUNDANCE AND GROWTH OF FISH IN PELAGIC AREAS

The capacity of a system to produce juvenile sockeye salmon is measured ultimately in the number of smolts produced. We have discussed our studies of the capacities of the spawning grounds. To locate and define factors that affect production of smolts in the rearing areas, we investigated the relation of the abundance of adult sockeye salmon to the abundance and growth of juveniles and associated species in the lakes.

Sockeye Salmon

The abundance of juvenile sockeye salmon in the lakes was measured with the pelagic tow net developed by Johnson (1956) and improved by Burgner (1958; footnote 9). In this study the standard unit of gear was a conical tow net 10 feet (3.1 m.) in diameter and 25 feet (8.3 m.) long. This net was pulled behind a pair of boats at night and fished with the center of the opening at two depths — 1.6 and 5 m. Modifications of the standard tow net were (1) a square opening of 9 feet (2.7 m.) and a length of about 25 feet (8.3 m.), used in the Wood and Kvichak systems; and (2) a square opening of 6 feet (1.8 m.) and a length of about 19 feet (5.8 m.), used in the Chignik system. The rate of catch is expressed in terms of the standard round opening 3.1-m. net pulled 1,500 feet (457 m.) in about 6 minutes.

Because we expected the abundance and growth of juvenile sockeye salmon and associated fishes would vary within lakes, we divided each lake into several sampling areas. The areas were not generally of uniform size, even within a lake. When we wish to discuss the average abundance or size of fish in a lake we must consider the relative contribution of each sampling area to the total population. We do this by a process of weighting in which we consider the portion of the total lake area in each sampling area and the relative abundance and size of the fish in the sampling area.[14] This process is repeated to compile an average for a system of more than one lake.

The mean catches of age 0 and age I and older sockeye salmon in tow nets (surface and deep tows combined) in the Wood, Kvichak, Naknek, Chignik, and Karluk systems, August 16 to September 15, are given in tables 17 and 18. Differences in abundance between systems within years were large (for example, 1961) as were

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[14] The following formulas yield the weighted average catch per tow and the weighted average length of fish.

$$C_W = \sum_{i=1}^{n} \left(\frac{a_i}{A}\right) c_i$$

$$L_W = \frac{\sum_{i=1}^{n} (c_i a_i)\, l_i}{\sum_{i=1}^{n} (c_i a_i)}$$

where C_W = weighted catch per tow for entire lake
c_i = average catch per tow for sampling area i
A = surface area of entire lake
a_i = surface area of sampling area i
L_W = weighted average length of fish in the lake
l_i = average length of fish in sampling area i

TABLE 17.—*Weighted mean catches of age 0 sockeye salmon per standard tow (surface and deep tows combined), August 16 to September 15, by lake and year, in lakes of the Wood, Kvichak, Naknek, Chignik, and Karluk systems, 1958-62*

System and lake	Surface area	Fish per tow 1958	1959	1960	1961	1962
	*Km.*²	*Number*	*Number*	*Number*	*Number*	*Number*
Wood system						
Lake Aleknagik	83	31.5	25.5	183.2	215.6	92.2
Lake Nerka	201	26.7	12.2	80.4	98.0	31.0
Lake Beverley	90	3.7	61.3	56.4	94.2	2.8
Lake Kulik	45	4.3	63.1	274.4	92.2	27.0
Little Togiak Lake	6	60.0	240.5	153.5	223.7	39.6
Kvichak system						
Iliamna Lake	2,622					5.0
Lake Clark	267					6.3
Naknek system (all lakes combined)	790				9.5	11.6
Chignik system						
Chignik Lake	22					28.9
					[1]180.0	[1]36.0
Black Lake	39					35.7
					[1]290.0	[1]56.0
Karluk system						
Karluk Lake	40				10.5	4.3

[1] Surface tows only.

TABLE 18.—*Weighted mean catches of age I and older sockeye salmon per standard tow (surface and deep tows combined), August 16 to September 15, by lake and year, in lakes of the Wood, Kvichak, Naknek, Chignik, and Karluk systems, 1958-62*

System and lake	Surface area	Fish per tow 1958	1959	1960	1961	1962
	*Km.*²	*Number*	*Number*	*Number*	*Number*	*Number*
Wood system						
Lake Aleknagik	83	1.9	0.4	0.3	17.2	3.8
Lake Nerka	201	1.2	.2	1.3	7.0	2.6
Lake Beverley	90	.2	.2	11.2	7.1	2.1
Lake Kulik	45	.8	.4	4.3	31.4	6.9
Little Togiak Lake	6	2.3	2.5	3.1	25.4	18.7
Kvichak system						
Iliamna Lake	2,622					20.2
Lake Clark	267					.0
Naknek system (all lakes combined)	790				2.0	5.5
Chignik system						
Chignik Lake	22					118.2
					[1]86.4	[1]125.9
Black Lake	39				.0	.0
						[1].0
Karluk system						
Karluk Lake	40				.9	1.2

[1] Surface tows only.

differences within systems between years (1961 and 1962 for all lakes of the Wood system). Some of these differences are examined in the following analyses for individual systems.

Wood system.—Preliminary use of the tow net to sample young sockeye salmon was started in lakes of the Wood system in 1957, and full-scale sampling began there in 1958. The relation between numbers of parent spawners per unit lake area and the production of age 0 sockeye salmon as measured by the geometric mean catch per standard tow (mid-August to mid-September) in each of the five Wood system lakes is presented for 1958-62 in figure 4. The relation between catch per tow of age 0 sockeye salmon and density of parent spawners seems to differ among lakes; hence, the data must be examined separately for each lake. A curve describing the relation between abundance of juveniles in the lake and density of parent spawners might be expected to start at zero, reach a maximum, and level off or decline as a result of increased mortality due to overcrowding of adults or eggs and larvae in the spawning areas or of young in the rearing areas. The relatively low catch of juveniles per tow in Little Togiak Lake and Lake

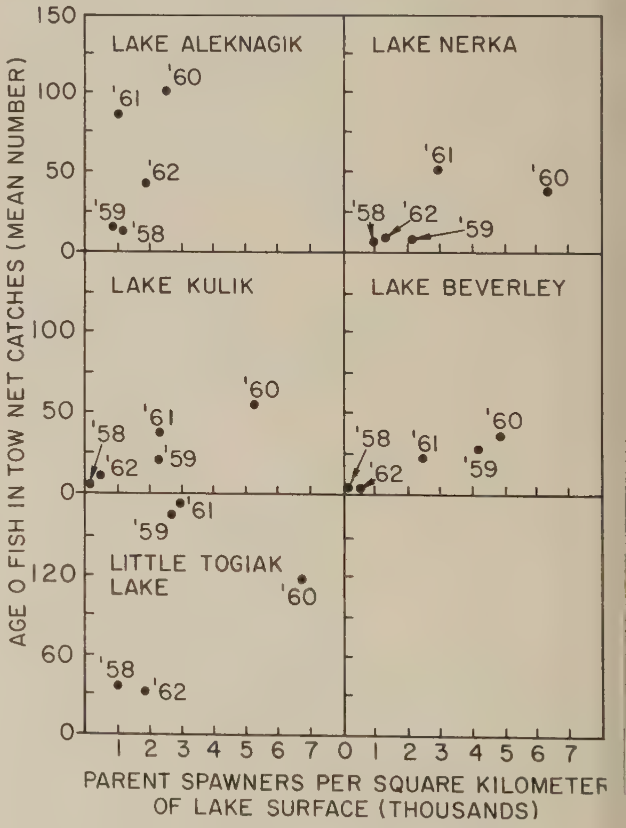

FIGURE 4.—Relation between abundance of age 0 sockeye salmon and numbers of parent spawners per unit lake area in each of the major lakes of the Wood system, 1958-62. The abundance of age 0 fish is the geometric mean of the abundance in tow net catches (mid-August to mid-September) weighted by depth and sampling area. The figure beside each point indicates the year of sampling.

Nerka at parent population densities approaching 7,000 spawners per square kilometer of nursery area (fig. 4) suggests decreased spawning efficiency or increased mortality of young at high population densities. There is some evidence of both.

The variation in the relations of abundance of juveniles to number of parent spawners per unit lake area in lakes of the Wood system is probably due to a combination of several factors: (1) errors in estimating numbers of spawners, (2) changes in survival from egg to juveniles available to the tow nets, and (3) random error in tow net sampling. Catches with the tow net indicate the same general abundance of juvenile salmon as do echo soundings recorded at the time of towing.

Evidence that the capacity of the nursery area may control the growth of fish in the Wood system is provided by data on growth of age 0 sockeye salmon in each of the four main Wood system lakes in 1958-62. The mean length of age 0 juveniles on September 1 is plotted against numbers of parent spawners per unit lake area for each lake (fig. 5). The inverse relation indicates that the progeny of large spawning populations grow slowly. Although the trend of the relation is obvious, the true shape of the line is probably obscured by five factors: (1) minor differences in growth potential (factors such as food availability and temperature) between lakes, (2) competition with variable numbers of yearling sockeye salmon from the previous year, (3) variability in the abundance of competitor species, (4) annual differences in climate that could affect the time of emergence, the length of growing season, and food supply, and (5) inaccuracies in estimates of numbers of spawners.

Differences are frequently observed in size of juvenile sockeye salmon between various parts of nursery lakes. These differences may be due to many factors including (1) real differences in growth rates, (2) differences in length of time the young have been in the lake, (3) differences in size of fry at hatching, and (4) differential rates of dispersion of faster and slower growing individuals. We have, therefore, used the term "apparent growth rate" in discussions of differences in size of juvenile sockeye salmon.

The apparent growth of young sockeye salmon in each of the three single-basin lakes in the Wood system is greatest in the east third and least in the west third of each lake (table 19). This relation holds for years of high and low population densities. Although the difference in apparent growth suggests basic differences in the growth potential of lake areas, progeny are smaller in the end of the lake that is closer to the major spawning grounds; and the differences in size within each lake may be the combined result of the longer lake residence of the early emerging fry and a more rapid dispersion of the larger fish.

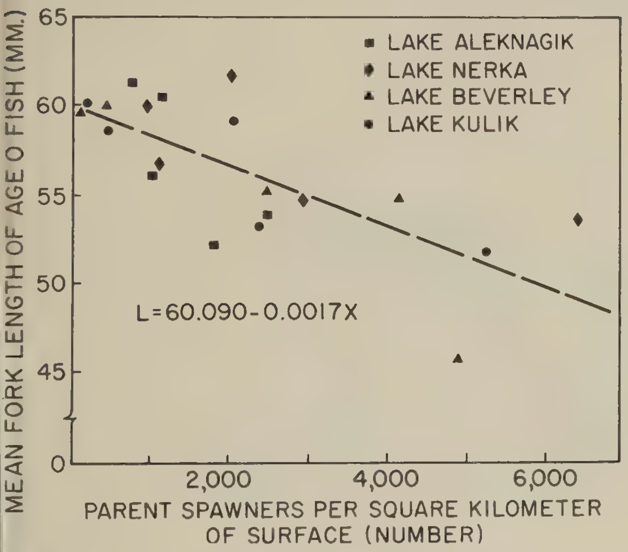

FIGURE 5.—Relation between mean fork length of age 0 sockeye salmon captured in tow nets, 1958-62, and abundance of parent spawners in lakes of the Wood system. The weighted mean fork length of the age 0 fish in each sample was adjusted to September 1 by applying a mean growth of 0.33 mm. per day, computed from growth data. The fish were measured after at least 24 hours in 10 percent Formalin.[15]

TABLE 19.—*Mean fork lengths[1] of age 0 sockeye salmon on September 1[2] in three single-basin lakes of the Wood system, 1958-62*

Year	Lake Aleknagik			Lake Beverley			Lake Kulik		
	West third	Middle third	East third	West third	Middle third	East third	West third	Middle third	East third
	Mm.	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*
1958	59.0	59.0	63.4	59.0	60.0	----	58.8	59.8	60.0
1959	57.5	62.7	60.8	50.5	57.3	61.2	61.5	60.6	58.8
1960	53.3	53.7	54.3	42.0	44.5	46.4	50.3	51.7	52.3
1961	52.2	57.5	57.5	51.1	52.2	59.2	51.7	52 8	55.1
1962	47.8	54.2	55.2	58.6	58.9	67.3	57.6	59.5	60.1
Mean	54.0	57.4	58.2	52.2	54.6	59.8	56.0	56.9	57.3

[1] After at least 24 hours in 10 percent Formalin.

[2] Lengths were adjusted to September 1 by applying a mean growth of 0.33 mm. per day computed from growth data.

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[15] Trade names referred to in this publication do not imply endorsement of commercial products.

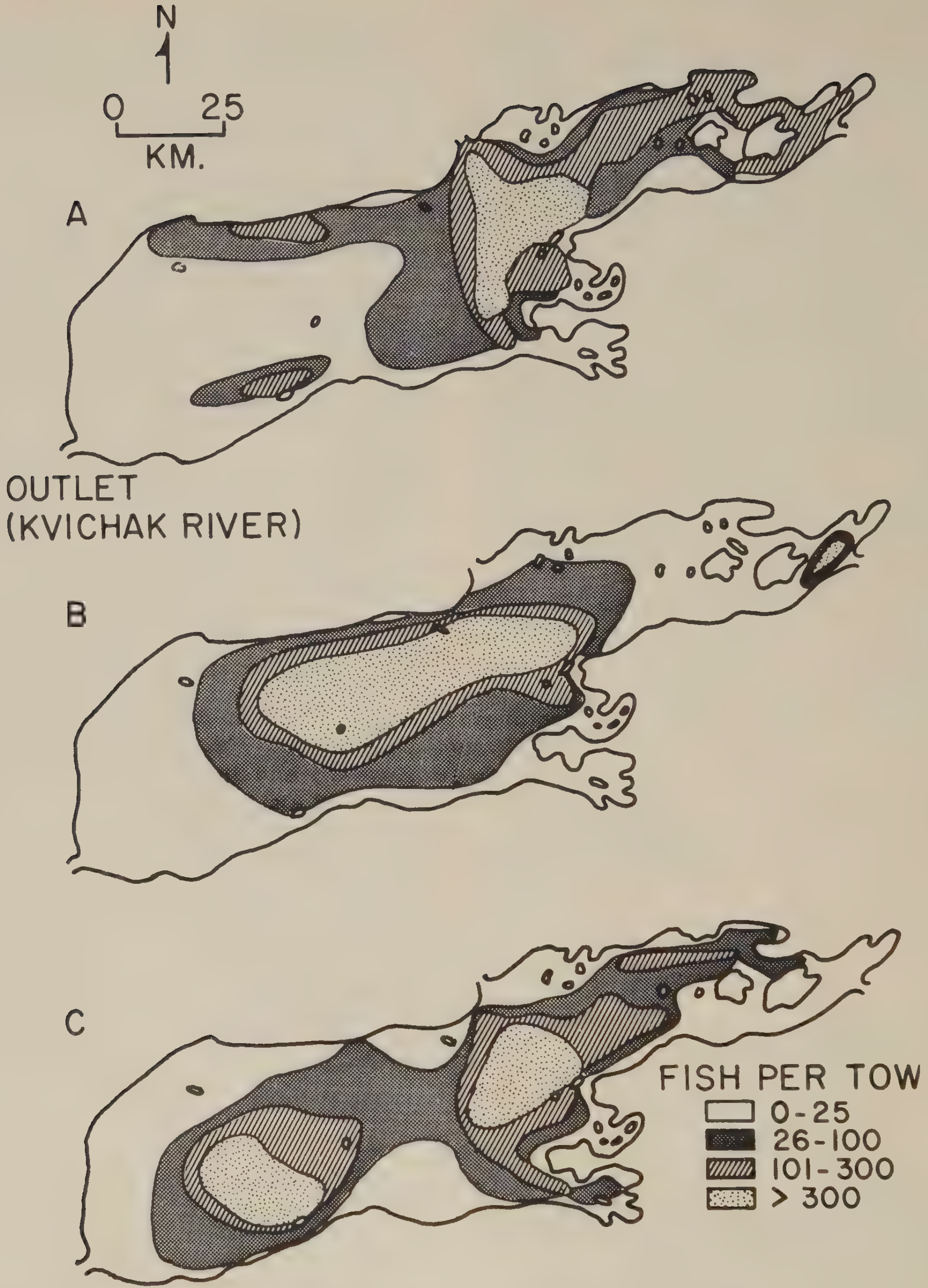
N
0 25
KM.
A
OUTLET
(KVICHAK RIVER)
B
C
FISH PER TOW
0-25
26-100
101-300
> 300

FIGURE 6.—Spatial distribution of juvenile sockeye salmon as indicated by the average catch per tow in Iliamna Lake, 1962. Catches in A (upper) are of age 0 fish caught between August 1 and September 15; in B (middle) are of age I fish caught between June 15 and July 31; and in C (lower) are of age I fish caught between August 1 and September 15.

Kvichak system.—Our most complete measure of the distribution and abundance of juvenile sockeye salmon in the Kvichak system is from tow net samples from Iliamna Lake in 1962 (fig. 6). The contour lines of density in the figure were determined by interpolation of the data on rate of catch between stations sampled and are not precise, but they illustrate the general distribution of the two age classes. The distribution and abundance changed during the summer and was different for age 0 and age I sockeye (fig. 6).

Most of the age 0 fish were in the eastern two-thirds of the lake from August 1 to September 15 —fig. 6A (the major spawning areas are in the eastern half of the lake).

Comparison of the distribution and abundance of age I sockeye salmon in early and late summer indicates a westerly movement, away from the principal spawning areas (fig. 6B and 6C). Age I juveniles had two centers of maximum concentration near the end of August—one in the west third and one in the middle third of the lake. These progeny of the 1960 escapement, therefore, occupied an area of the lake during their second summer (1962) that is probably not heavily used when most of the juveniles migrate to sea as age I smolts in early summer.

We found gradients in proportion of young-of-the-year and yearling sockeye salmon in the tow net catches in 1962 and in the average length of each age group from the outlet of the system to distant points in the system in catches made with an Isaacs-Kidd midwater trawl in 1961 and tow nets in 1962 (table 20). Yearling sockeye salmon were essentially absent from catches in 1961, but in 1962 they made up about 90 percent of the catches in the third of the lake closest to the outlet, about 85 percent in the middle third, and 45 percent in the most distant third. None were taken in Lake Clark. The average lengths of both age classes were greater nearer the outlet and less at the more distant points both years.

A strong gradient was found at the end of August 1962 in the mean length of age I sockeye salmon from three areas of Iliamna Lake. The average lengths in the east, middle, and west thirds of the lake were 81.5, 88.1, and 99.6 mm., respectively. Since spawning is most limited in the west end of the lake, the gradient is thought to be due to the more rapid or earlier migration of the larger and possibly older fish. By the following spring (1963) the westward movement of these fish (now age II smolts) must have been completed because most of them migrated in the first few days after the ice in the lake broke up.

TABLE 20.—*Age class composition and mean fork length of juvenile sockeye salmon on September 1 in various areas of the Kvichak system, 1961-62. The fish were captured with an Isaacs-Kidd midwater trawl in 1961 and in a 6-foot-square opening tow net in 1962. Original measurements were made of live fish and these data converted to preserved fish equivalents*

Area	1961				1962			
	Young-of-the-year		Yearlings		Young-of-the-year		Yearlings	
	Frequency	Average length	Frequency	Average length	Frequency	Average length	Frequency	Average length
	Percent	*Mm.*	*Percent*	*Mm.*	*Percent*	*Mm.*	*Percent*	*Mm.*
Iliamna Lake								
Igiugig					0	----	100	98.6
Shoulderblade					0	----	100	96.3
Grassy					81	56.6	19	90.5
Middle Talarik					24	56.1	76	91.5
Chekok					0	----	100	93.1
Dennis					20	57.8	80	80.2
Upper Talarik	100	59.7	0	----	18	54.7	82	85.3
Ten-Mile Island					15	50.6	85	77.9
Middle Island					8	53.6	92	81.9
Gibraltar					26	52.7	74	88.4
Kakhonak Bay					3	----	97	89.1
Intricate Bay					22	53.6	78	83.8
Tommy Point	100	54.3	0	----	25	50.7	75	79.2
Iliamna	100	53.9	0	----	56	50.2	44	79.5
Triangle Island	100	52.4	0	----	30	52.9	70	77.0
Knutson Bay	100	46.2	0	----	66	52.5	34	76.7
Pedro Bay	100	51.7	0	----	78	48.8	22	76.7
Pile Bay	100	50.2	0	----	75	48.4	25	74.6
Lake Clark								
Lower lake					100	51.3	0	----
Middle lake					100	46.3	0	---

Naknek system.—The interlake migration of sockeye salmon in the Naknek system during their first summer influences the relation between the abundance of young salmon in each lake at the end of the summer and the number of adults in the parent escapement to each lake. Data collected with tow nets in 1962 have been used to estimate a systemwide average catch per tow by day, weighted by area of each lake, for July 11 to August 29. Sampling was not daily. Missing data for an area were derived by averaging the figures of the most recent preceding and the first following sampling in that area. These weighted figures were combined for all areas each date to find the hypothetical catch per tow for the entire system and were smoothed by a moving average of three. The data (fig. 7) show a gradual increase in abundance of age 0 fish while recruitment from the spawning grounds exceeds mortality, a general leveling of the curve from July 20 to August 10, and a decline in rate of catch per tow after August 10. The curve

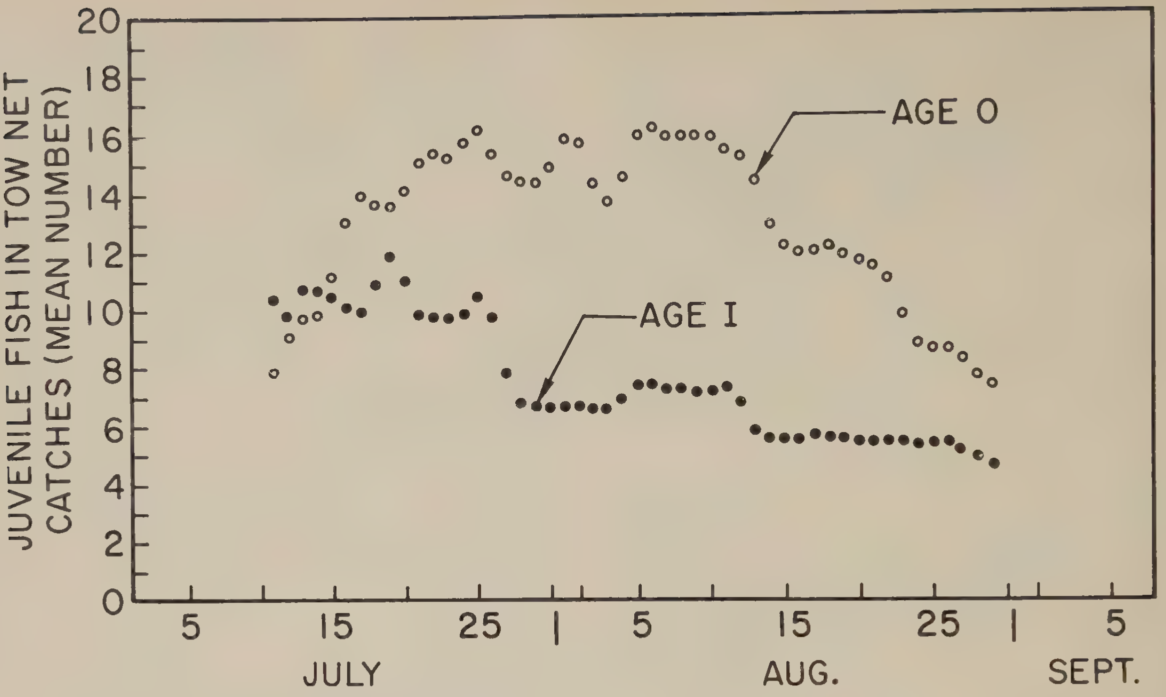

FIGURE 7.—Weighted daily mean catch of juvenile sockeye salmon per tow in Naknek system, all lakes combined, 1962. The mean catch for the system has been weighted by the size of each sampling area, and the daily estimates have been smoothed by a moving average of three—(A + 2B + C) ÷ 4.

would be somewhat higher if data from North Arm, which is not involved in the interlake movement, were omitted. The weighted mean catch of age I juveniles for the system was greatest in the earliest tows, July 11 to 20, and declined gradually during the summer.

Within lakes of the Naknek system we found a wide range in numbers of adult spawners per unit area of lake and also in the abundance of their progeny. Coville Lake had an escapement of about 6,600 adults per square kilometer in 1961; Brooks Lake had 267; and North Arm had 55. In July 1962 (before the presmolt interlake migrations) the average number of age 0 sockeye salmon in tow net catches was 150 in Coville Lake, 2 in Brooks Lake, and 0.5 in North Arm. The abundance of spawning adults (table 15) and of age 0 juveniles in these three lakes nearly cover the range found in southwestern Alaska.

Studies of juvenile salmon in the Naknek system have run too few years to determine the relation between the abundance of age 0 sockeye salmon and the size of the parent population. The escapement to the Naknek system in 1960 was 828,000 spawners, and the average catch of age 0 sockeye per tow in 1961 (in late August) was about 9.5. The escapement in 1961 was about 350,000, and the average catch per tow in 1962 was about 11.6.

The age composition and mean fork lengths of juvenile sockeye salmon on September 1 are presented for the Naknek and Karluk systems in table 21 by lake or sampling area. The average lengths of age 0 sockeye salmon in the Naknek system were greater in 1962 than in 1961, although the numbers of age 0 and age I fish in the system were essentially the same, as indicated by tow net catches in 1961 and 1962 and the smolt emigration in 1962 and 1963. The average catches per tow were 9.5 and 11.6 age 0 fish on August 20, and the smolt migrations were 8 million age I and 8 million age II in 1962 and 6 million age I and 8 million age II in 1963.

The year-to-year variation in basic productivity of the lakes of the Naknek system may cause marked differences in growth of juvenile sockeye salmon independent of their abundance. As was shown earlier in this report, basic productivity was comparatively low in 1961 and high in 1962. The resulting apparent growth of juvenile sockeye salmon reflected these differences.

The variation among mean lengths of age 0 sockeye salmon in the several basins of the Nak-

TABLE 21.—*Age composition and calculated*[1] *mean fork lengths*[2] *on September 1 of age 0 and age I sockeye salmon captured in tow nets in lakes of the Naknek and Karluk systems, weighted by surface area and catch per tow, 1961-62*

System, lake, and year	Age 0 fish: Frequency	Age 0 fish: Mean fork length	Age I fish: Frequency	Age I fish: Mean fork length
	Percent	*Mm.*	*Percent*	*Mm.*
Naknek system				
Coville Lake				
1961	100.0	54	0	----
1962	100.0	60	0	----
Grosvenor Lake				
1961	100.0	46	0	----
1962	100.0	52	0	----
Naknek Lake				
North Arm				
1961	-------	-------	-------	------
1962	62.5	56	37.5	98
Iliuk Arm				
1961	84.1	57	15.9	78
1962	69.2	61	30.8	91
South Bay				
1961	64.3	47	35.7	86
1962	26.0	63	74.0	85
West End				
1961	75.1	65	24.9	89
1962	91.8	69	8.2	---
Brooks Lake				
1961	96.3	51	3.7	----
1962	97.1	60	2.9	----
Karluk system				
Karluk Lake				
1961	88.7	40	11.3	83
1962	81.9	49	18.1	76

[1] Curves describing the average length were calculated for each lake each summer; only those data involving 10 or more fish were used.

[2] After at least 48 hours, preservation in 10 percent Formalin.

TABLE 22.—*Calculated mean fork length of age 0 sockeye salmon from the upper end of Naknek system to outlet on September 1, 1962*

Sampling area	Fork length
	Mm.
Coville Lake	
Upper half	56
Lower half	60
Coville River	61
Grosvenor Lake	52
Grosvenor River	63
Naknek Lake	
Iliuk Arm	
Upper third	57
Middle third	63
Lower third	61
South Bay	
Upper third	61
Middle third	66
Lower third	--
West End[1]	69

[1] Does not include samples from the small basin in the northwest corner of Naknek Lake.

nek system (table 22) seems to reflect the results of a combination of at least three factors: (1) movement of the large fish first in the interlake migrations, (2) midseason recruitment of recently emerged fry (especially evident in Grosvenor Lake), and (3) differences in productivity of waters. The average size of juveniles taken in tow nets in Coville Lake increased from the upper to the lower end and increased again in juveniles taken in fyke nets as they migrated from Coville Lake to Grosvenor Lake. The juveniles captured in fyke nets in Grosvenor River were larger than those taken in tow nets in the lake. In the next basin downsystem, Iliuk Arm, smaller fish were more abundant at the inlet (upper third) even though the larger juveniles that migrated from Grosvenor Lake enter this end. The average size was the same in the upper third of South Bay and the adjacent area of Iliuk Arm but increased toward the outlet of the lake.

Chignik system.—The number of parent spawners per unit lake area in the Chignik system was greater in 1960 than in 1961, and, correspondingly, age 0 progeny were more abundant in 1961 than in 1962. The mean lengths of the age 0 progeny on September 1 were less in the year of greater abundance (table 23). The relations are similar to those in the Wood system. In the Chignik lakes, however, the apparent growth of progeny at similar densities of spawners and progeny is better than in the lakes of the Wood system; this difference may be due to a combination of richer nursery areas and fewer competitors in the Chignik lakes.

Karluk system.—The escapement of sockeye salmon in Karluk Lake was greater in 1960 than in 1961, and, correspondingly, age 0 progeny were more abundant in 1961 than in 1962. In 1960 about 349,000 adults entered the system and the average catch per tow of age 0 fish in 1961 was 8.9 from August 16 to September 15. The escapement in 1961 was about 297,000, and the average catch per tow in 1962 was 4.3.

The average length of age 0 sockeye salmon in Karluk Lake was greater in 1962 than in 1961 (table 21). The juveniles were larger in the year of lesser abundance (1962), so it might be assumed that the size of age 0 fish is density-dependent. But because of the long period of recruitment of recently emerged fry into the lake —caused by the extended spawning period (4-5 months)—the mean size of young-of-the-year at the end of the summer is based on fish that may differ in age by many weeks. Differences in the abundance of early- and late-spawning stocks might result, therefore, in apparent but non-

TABLE 23.—*Parent escapement of sockeye salmon, as numbers per square kilometer of lake, average catch of age 0 progeny per standard tow, and average length of age 0 progeny in Black and Chignik Lakes, 1960-61*

Lake and year of spawning	Parent spawners per square kilometer	Age 0 progeny	
		Average catch per tow	Average fork length
	Number	*Number*	*Mm.*
Black Lake			
1960	6,128	180	58.9
1961	3,359	36	69.0
Chignik Lake			
1960	16,773	90	46.9
1961	12,545	56	47.2

existent differences in growth rates between seasons.

For Karluk Lake, both the average catches of juvenile sockeye salmon in tow nets (tables 17 and 18) and the average lengths for each age group (adjusted to September 1) were among the lowest recorded in this study (tables 19, 20, 21).

Associated Species

Several species of fish are captured frequently with juvenile sockeye salmon in the tow nets. The species and abundance vary from system to system. The most common in order of general abundance are threespine stickleback, ninespine stickleback, pond smelt, and pygmy whitefish.

The threespine stickleback is the most abundant species associated with young sockeye salmon in the Wood, Kvichak, Naknek, Chignik, and Karluk systems (table 24). Both species tend to concentrate near shore in the spring and spread toward the pelagic area of the lake as the season advances. Similarities in the food habits of these two species have been well established (Rogers, 1961).

Wood system.—The average abundance of threespine sticklebacks in tow net catches in the Wood system varied in 1958-62 (table 24) almost as much as, but seemingly independently of, that of juvenile sockeye salmon. In some years the biomass of the sticklebacks, as indicated by abundance in tow net catches, has approached or exceeded that of the juvenile salmon.

The average rate of growth of threespine sticklebacks varies from year to year and usually in the same direction as that of the juvenile sockeye salmon (fig. 8). The slowest growth of threespine sticklebacks (and of juvenile sockeye) generally is in years of greatest abundance

TABLE 24.—*Weighted mean catch of sticklebacks per standard tow (surface and deep tows combined), August 16 to September 15 in lakes of the Wood, Kvichak, and Chignik systems, 1958-62*

Species, system, and lake	Fish per tow				
	1958	1959	1960	1961	1962
	Number	*Number*	*Number*	*Number*	*Number*
Threespine sticklebacks					
Wood system					
Lake Aleknagik	81.4	310.2	85.2	62.4	188.0
Lake Nerka	51.5	53.4	26.4	24.0	30.2
Lake Beverley	133.0	51.2	53.7	22.0	3.0
Lake Kulik	285.6	21.9	14.8	13.2	14.1
Little Togiak Lake	113.4	106.3	25.2	51.0	65.6
Kvichak system					
Iliamna Lake					27.8
Lake Clark					.0
Chignik system					
Chignik Lake				[1] 4.1	3.8 [1] 5.0
Black Lake				[1] 196.4	170.3 [1] 162.4
Ninespine sticklebacks					
Chignik system					
Chignik Lake				[1] 6.6	7.2 [1] 7.0
Black Lake				[1] 7.2	32.2 [1] 28.9

[1] Surface tows only.

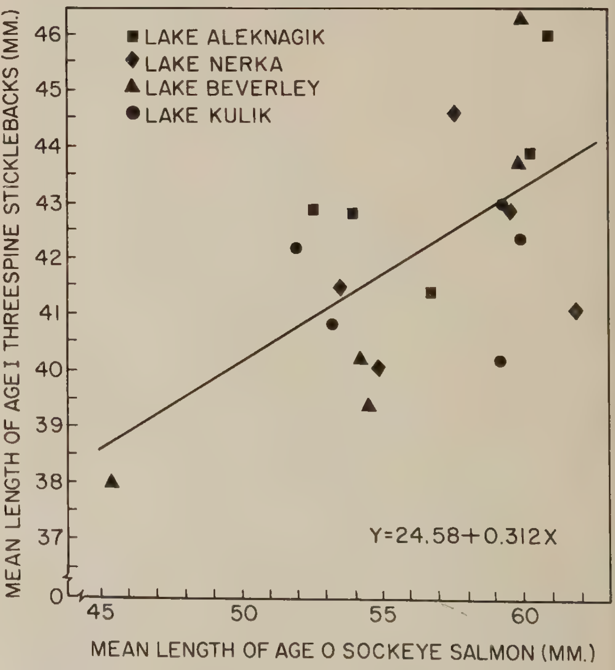

FIGURE 8.—Relation between mean length of age I threespine sticklebacks and mean length of age 0 sockeye salmon taken in tow nets each year, 1958-62, in each of four lakes of the Wood system. The mean lengths of both species have been weighted and adjusted to September 1.

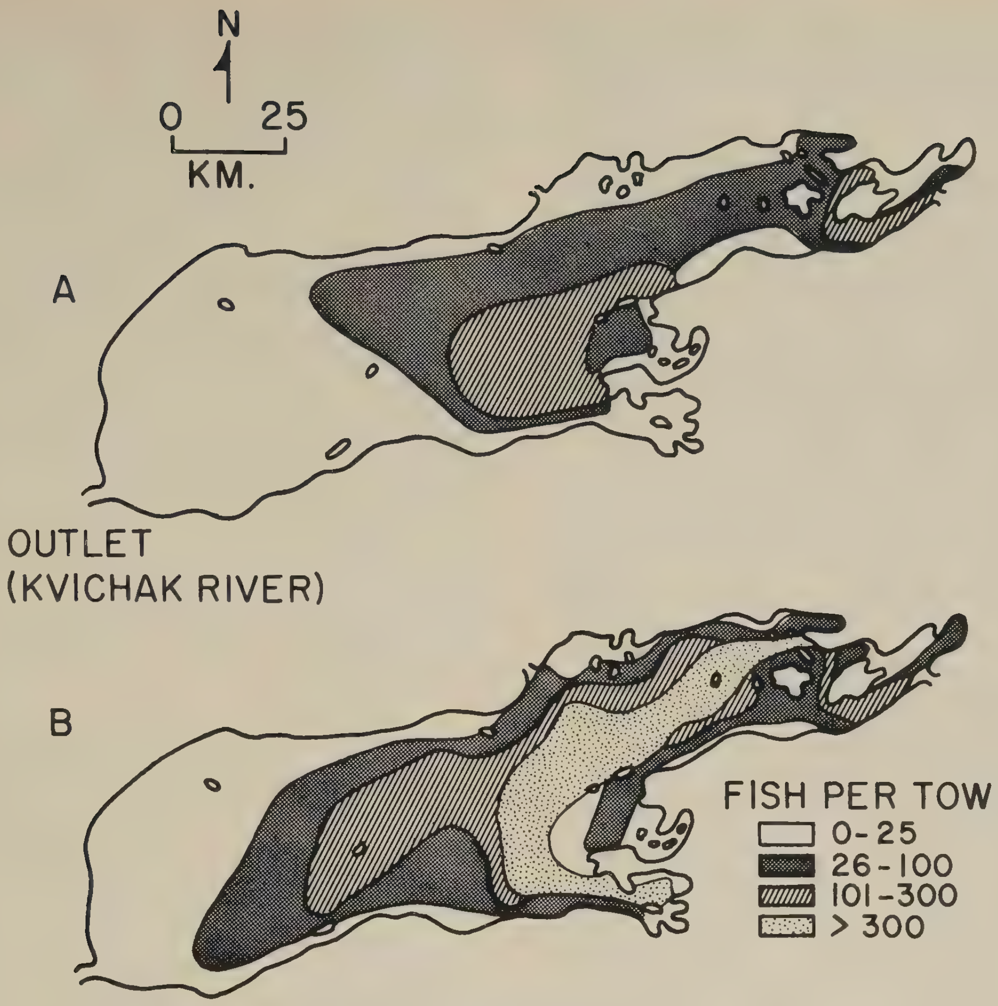

FIGURE 9.—Abundance and distribution of threespine sticklebacks in Iliamna Lake, 1962, as indicated by average catches in tow nets. Catches in A (upper) made June 15 to July 31; in B (lower) August 1 to September 15.

of juvenile salmon. The smaller size of threespine sticklebacks and the juvenile sockeye salmon in the western ends of the lakes of the Wood system suggests that the same factors influence the growth of both species.

Kvichak system.—The abundance and distribution of threespine sticklebacks in Iliamna Lake in tow net catches in 1962 before and after August 1 are shown in figure 9. The abundance contours of figure 9 are intended only to indicate the general situation in the pelagic areas.

Threespine sticklebacks were most abundant in the pelagic areas before August 1 in the upper bays of Iliamna Lake and in an area west of but adjacent to the Kakhonak-Intricate Bay complex (fig. 9A). After August 1, threespine sticklebacks were abundant over a much larger area (fig. 9B). The increased abundance in a larger area must be caused by a seasonal movement of sticklebacks from the littoral zone. Comparisons of the seasonal distribution of threespine sticklebacks and of age 0 and age I sockeye salmon suggest that competition could be greater between sticklebacks and age 0 salmon than between sticklebacks and age I salmon.

No threespine sticklebacks were caught in the limited tow net sampling in Lake Clark in 1962 or 1963.

Naknek system.—The species and abundance of fish caught in the Naknek system in tow nets with juvenile sockeye salmon varied among the lakes (table 25). Threespine sticklebacks were caught in tow nets in all of the lakes and were more abundant than all of the other species,

TABLE 25.—*Weighted mean catch per standard tow (surface and deep tows combined) of species associated with juvenile sockeye salmon, August 16-31, in lakes of the Naknek and Karluk systems, 1961-62*

Species, system, and lake	Fish per tow	
	1961	1962
	Number	*Number*
Threespine sticklebacks		
Naknek system		
Coville Lake	8.0	85.5
Grosvenor Lake	.2	.0
Naknek Lake		
North Arm	.1	3.6
Iliuk Arm	3.4	6.1
South Bay	9.3	12.0
West End	647.8	54.8
Brooks Lake	[1].0	.1
Karluk system		
Karluk Lake	63.9	115.1
Ninespine sticklebacks		
Naknek system		
Coville Lake	8.8	34.4
Grosvenor Lake	.1	.0
Naknek Lake		
North Arm	.0	.2
Iliuk Arm	.2	.8
South Bay	.9	15.0
West End	65.0	29.3
Brooks Lake	.1	.2
Karluk system		
Karluk Lake	.0	.0
Pond smelt		
Naknek system		
Coville Lake	91.0	49.5
Grosvenor Lake	.2	.0
Naknek Lake		
North Arm	.0	.1
Iliuk Arm	.0	.4
South Bay	.1	.1
West End	.1	.6
Brooks Lake	.0	.0
Karluk system		
Karluk Lake	.0	.0
Pygmy whitefish		
Naknek system		
Coville Lake	.0	.2
Grosvenor Lake	.0	.0
Naknek Lake		
North Arm	.0	.1
Iliuk Arm	.0	.1
South Bay	.5	.0
West End	.0	.0
Brooks Lake	.3	.2
Karluk system		
Karluk Lake	.0	.0

[1] Less than 0.05.

except pond smelt in Coville Lake. Although ninespine sticklebacks were distributed the same as threespine sticklebacks, they were generally less abundant. Pond smelt were taken in tow nets in all basins of the Naknek system except Brooks Lake but were abundant only in Coville Lake. Pygmy whitefish, which are basically benthic, were rarely taken in the tow net catches but were highly abundant in trawl catches from Brooks Lake. Areas of the Naknek system that yielded the largest catches of juvenile sockeye salmon or the fastest growing juveniles or both also yielded the largest catches of associated species.

Chignik system.—In the Chignik system, threespine sticklebacks were about 30 times as abundant in tow net catches in Black Lake as in Chignik Lake (table 24). The sticklebacks may be unable to compete successfully with the large populations of young sockeye salmon that often occur in Chignik Lake. Ninespine sticklebacks were slightly more abundant than threespine sticklebacks in Chignik Lake but were less abundant in Black Lake (table 24). Pond smelt were not as abundant as sticklebacks but occurred frequently in tow net catches in both lakes. Other species were seldom taken.

Karluk system.—The threespine stickleback was the only species other than juvenile sockeye salmon captured in tow nets at Karluk Lake (table 25), and sticklebacks were much more abundant than juvenile salmon in all sampling with all gear.

PREDATION ON JUVENILE SOCKEYE SALMON

Predation on juvenile sockeye salmon in fresh water occurs during their emergence, migration from the spawning areas, and residence in and migration from the nursery lakes. Predation by birds and fish is often very obvious and dramatic in southwestern Alaska.

A few studies and many general observations have been made of the relative intensity of predation by various animals in several systems. Most of the predators to be mentioned are present in all the sockeye salmon systems in southwestern Alaska.

In the Mainland Systems the Arctic char is the most significant predator on sockeye salmon, but many others do occur.

In the Igushik, Snake, Wood, and Kvichak systems the Arctic char is the fish that eats the most sockeye salmon juveniles—as migrating fry, as residents in the lakes, and as migrating smolts. In the Nuyakuk system, lake trout are more abundant than Arctic char and consume more young sockeye salmon. Other fish predators observed to eat young sockeye salmon in these lake systems are juvenile coho salmon, northern pike, grayling, and rainbow trout. During the smolt migrations, Arctic Terns *(Sterna paradisaea)* and Bonaparte's Gulls *(Larus philadelphia)* prey on sockeye salmon in the rivers connecting lakes and in the trunk river.

Several species prey on juvenile sockeye salmon at different stages in the Naknek system. Dolly Varden are abundant and in several areas feed actively on sockeye salmon fry during their emergence and migration. Juvenile coho salmon, present throughout the system, have been observed feeding on sockeye salmon fry in Brooks Lake. Presmolt sockeye salmon migrate out of Coville Lake in late summer day and night; at that time predation by lake trout, Arctic Terns, and Bonaparte's Gulls is very obvious.

Dolly Varden and rainbow trout prey on migrating smolts in the Naknek River. Other possible fish predators in the Naknek system are Arctic char, northern pike, Arctic grayling *(Thymallus arcticus)*, and sculpins (*Cottus* spp.).

Dolly Varden and juvenile coho salmon both prey on juvenile sockeye salmon in the Chignik system (Roos, 1960), but the predation by coho salmon seems to be the more significant (Roos, 1959).

The Karluk system has large numbers of Dolly Varden and Arctic char (DeLacy and Morton, 1943), which may be serious predators of juvenile sockeye salmon.

The effectiveness of predators in keeping competitors of sockeye salmon in check is unknown but may be important. In the Wood system, for example, threespine sticklebacks are an important item in the diet of Arctic char.

The destruction of a constant number of juvenile sockeye salmon by predators each year would help sustain and perhaps reinforce the cyclic nature of some runs to the Bristol Bay systems. A constant annual demand would have a greater effect in years of low abundance of juvenile sockeye salmon. Such an effect is suggested for the sockeye salmon of Shuswap Lake of the Fraser system (Ward and Larkin, 1964).

REPRODUCTIVE RELATIONS OF POPULATIONS IN FRESH AND SALT WATER

The relations between numbers of smolts produced and numbers of adults in the parent escapements (described by the reproductive curve) are highly variable, even within a system, because they are determined by the interaction of many physical and biological factors. In this section we consider the relations between numbers of adults in the parent escapement and their progeny in terms of numbers, size, and age of smolts migrating to sea, and numbers of adults returning from the sea (catch and escapement).

RELATION BETWEEN NUMBERS OF SMOLTS AND NUMBERS OF ADULTS IN PARENT ESCAPEMENT

The major purpose of studies of the numbers of smolts produced by various numbers of spawners is to define the relation and interpret it to make estimates of optimum escapement (in terms of numbers of smolts) either directly or with the aid of ancillary information.

Smolt migrations were sampled with fyke nets in the trunk rivers. The abundance is expressed in index points for the Wood and Kvichak Rivers and in numbers of fish for the Naknek, Ugashik, and Karluk Rivers. The methods of counting the escapement of adults were described earlier in this report.

The index method of estimating production of smolts requires the use of standard fishing gear, site, and effort. The numbers of smolts captured are then given value in relation to the catches of a base year which has an arbitrary value of 100 index points. This method is used in the Kvichak system (Kerns, 1961) and the Wood system (Burgner, 1962). It yields data comparable between years within a system but not between systems.

The estimates of numbers of smolts produced by a system were based on a regular system of sampling. Many fishing sites were set up across the width of the river, and fyke nets were fished for a fixed period of time once a day in each site in random order. The sequence of fishing sites and times of day was a modified Latin-square design (Cochran and Cox, 1957). Catches were classified according to site, time of day, and date —factors considered to have the greatest influence on variability of the individual catches. Estimates of the total numbers of smolts in the annual migrations were obtained by expanding the mean catch per standard fishing period according to the number of potential fishing sites in the width of the river and the number of fishing periods in the season. We used this method to estimate the numbers of smolts migrating in the Naknek and Ugashik systems.

The age composition of the smolts in each migration was estimated from length-frequency measurements or scale samples taken during the season and weighted by magnitude of fyke net

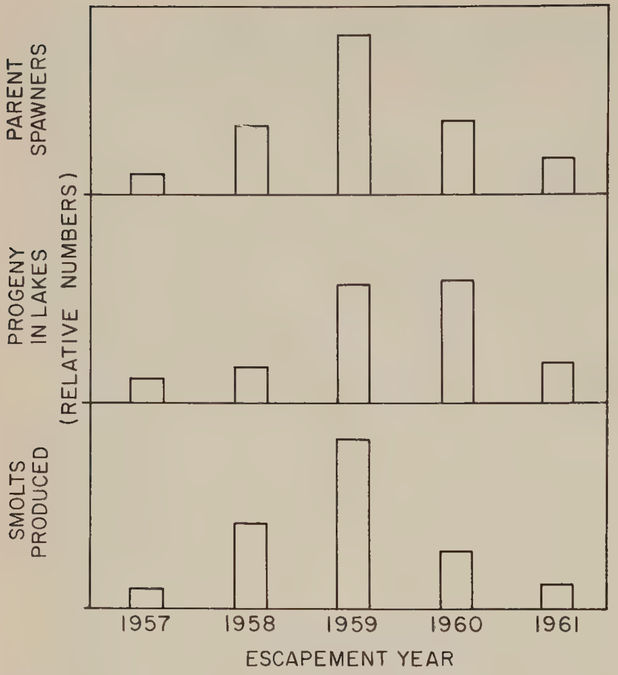

FIGURE 10.—Comparison of relative size of sockeye salmon escapement, abundance of progeny in lakes (based on tow net catches), and smolts in Wood River (based on fyke net catches), Wood system, parent escapement years of 1957-61.

catches for the day (or days) on which the samples were taken. Smolts were measured in the fresh state soon after capture.

Wood System

The Wood system showed two general levels of production of smolts (index points) per 1,000 adults in the escapement, the high level (1951 to 1954) was 0.50 to 1.87 index points (base of 1.00), and the low level (all other years from 1949 to 1961) was 0.10 to 0.27 (table 26). The cause of the considerable difference between the two levels is not known—it might be due to unusually good conditions for survival in the lakes or to a consistent error in indexing smolt abundance from 1951 to 1954.

The index estimates of smolt abundance in the Wood system for later years, 1957-61, can be checked against estimates of abundance at two other stages of fresh-water residence—the relative size of escapements and the abundance of progeny in the lakes (based on tow net samples in late August). The three estimates of abundance had the same general changes from 1957 through 1961 (fig. 10).

TABLE 26.—*Number of sockeye salmon in escapements and abundance, age composition, and mean length of smolts produced, by year of spawning, Wood system, 1949-61*

[Size of escapements for years 1949-52 based on stream surveys only]

Year of spawning	Adults in escapement	Smolts produced	Smolts produced per 1,000 spawners	Age composition of smolts: Age I	Age composition of smolts: Age II	Mean length [1] of smolts: Age I	Mean length [1] of smolts: Age II
	Thousands	*Index points*	*Index points*	*Percent*	*Percent*	*Mm.*	*Mm.*
1949	101	10	0.10	----	----	[2] 91	----
1950	452	115	.25	87	13	[2] 87	[2] 103
1951	458	299	.65	94	6	[2] 86	107
1952	227	425	1.87	99	1	87	102
1953	516	290	.56	75	25	85	95
1954	571	286	.50	89	11	82	93
1955	1,383	215	.16	62	38	77	102
1956	773	154	.20	97	3	82	105
1957	289	59	.20	97	3	88	114
1958 [3]	960	255	.27	86	14	88	102
1959 [4]	2,209	508	.23	95	5	82	98
1960 [4]	1,016	167	.16	92	8	80	102
1961 [4]	461	82	.18	92	8	83	104

[1] Fork length of live anesthetized fish.

[2] Based on several samples taken during the main migration season but not weighted by catch.

[3] Age composition and mean length approximated in 1958 because of difficulty in determining age of smolts.

[4] Smolt data furnished by Alaska Department of Fish and Game for 1961-63.

The relation between numbers of smolts produced and numbers of adults in the parent escapement in the Wood system (fig. 11) is nearly linear in years when production per spawner was low (years other than 1951-54). Since the cause of the high rate of smolt production from 1951-54 is unknown, all points on figure 11 must be given equal weight, and, therefore, optimum escapement in terms of smolt production cannot be determined from these data.

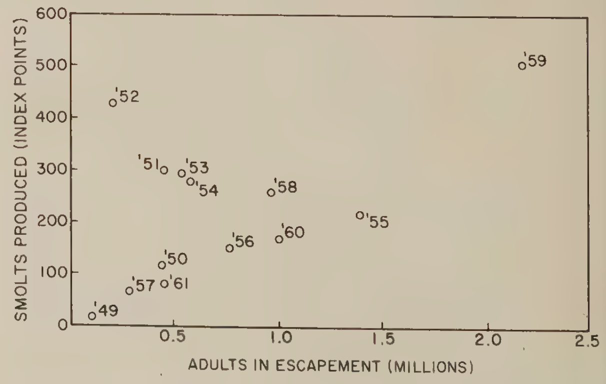

FIGURE 11.—Relation between smolt production (indexed by catches made in fyke nets in Wood River) and number of sockeye salmon in parent escapement, 1949-61, Wood system. The figure beside each point is the year of the parent escapement.

TABLE 27.—*Number of sockeye salmon in escapements and abundance, age composition, and mean length of smolts produced, by year of spawning, Kvichak system, 1952-60* [1]

[Size of escapements for 1952-54 based on stream surveys]

Year of spawning	Fish in escapement	Smolts produced	Smolts produced per 1 million spawners	Age composition of smolts		Mean length [2] of smolts	
				Age I	Age II	Age I	Age II
	Thousands	*Index points* [3]	*Index points* [3]	*Percent*	*Percent*	*Mm.*	*Mm.*
1952	5,970	----	----	----	----	----	109
1953	321	1.95	6.1	28	72	89	116
1954	241	1.15	4.8	78	22	92	120
1955	251	2.65	10.6	23	77	96	114
1956	9,443	181.32	19.2	54	46	84	99
1957	2,843	19.14	6.7	13	87	80	108
1958	535	2.15	4.0	86	14	91	118
1959	680	2.96	4.4	27	73	93	110
1960	14,630	[4] 157.38	10.8	22	78	82	98

[1] Abundance and length data for age II smolts from the 1958 escapement and age I smolts from the 1959 escapement supplied by Alaska Department of Fish and Game.

[2] Fork length of live anesthetized fish.

[3] Based on 24-hour catches.

[4] Marriott (1965).

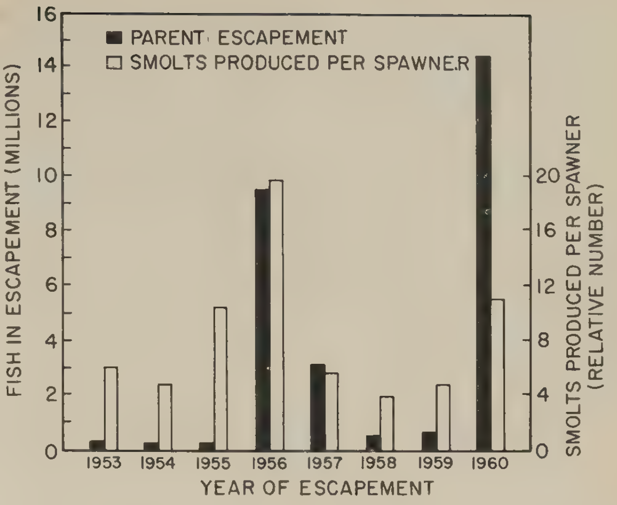

FIGURE 12.—Number of sockeye salmon in parent escapement and relative numbers of smolts produced per spawner, by year of escapement, in the Kvichak system, 1953-60.

Kvichak System

Data on smolts produced (index points) and the numbers of adults in the parent escapement in the Kvichak system are presented in table 27 for 1953-60.

The production of smolts per spawner in the Kvichak system does not follow the classic reproduction curves described by Schaefer (1954), Beverton and Holt (1957), and Ricker (1958). Reproduction curves are based on the assumption that the return per spawner is inversely related to the numbers of spawners, but in the Kvichak system the maximum production of smolts per spawner was produced by the relatively large escapement of 9.4 million in 1956 (table 27, fig. 12). The escapement of 14.6 million adults in 1960 apparently produced smolts at a lower rate per spawner[16] than that of 1956 but still greater than in most years of low escapement.

We assume that two reproduction curves are applicable in the Kvichak system—one for large escapements or "peak" years (over 5 million fish) and one for small escapements or "low" years (5 million fish or fewer). Two derived points are available for calculating the relation between smolt production and large escapements, namely the most recent peak years of the cycle, 1956 and 1960. Axiomatically, the reproduction curve includes the origin. A compound exponential curve of a type suggested by Ricker (1958) fitted to these three points necessarily produces a flat dome. These data indicate that the optimum escapement is less than the 1956 escapement, i.e., less than 9.4 million spawners (footnote 16).

We conclude that our estimate of the number of smolts produced by the 1960 escapement was too low, and, consequently, our estimate of the optimum escapement for peak years is also too low and will be raised as more data become available.

Naknek System

Estimates were made of the number of smolts produced in the Naknek system from each escapement in 1954-61 (table 28). Within these years the escapements ranged from 0.28 to 2.23 million.

The number of smolts produced increased as the escapement increased, up to an escapement of about 1 million (fig. 13). Beyond this point the number of smolts tended to level off (at about 14 million smolts) or decline.

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[16] The extraordinarily large return of sockeye salmon to the Kvichak system in 1965 from the 1963 smolt run was unexpected. The smolt production from the 1960 escapement must have been greater than that indicated by the fyke net catches (shown as index points in table 27 and figure 12) because the return was disproportionately large, and ocean survival was not unusually high for sockeye salmon from other systems during this period. Intermittently occurring ice floes in the Kvichak River between May 15 and June 1, 1963, made it difficult to fish the fyke nets properly (footnote 4, table 27).

TABLE 28.—*Number of sockeye salmon in each escapement and number of smolts produced, by year of spawning, Naknek system, 1954-61*

Year of spawning	Fish in escapement	Smolts			
		Age I	Age II	Age III	Total
	Thousands	*Millions*	*Millions*	*Millions*	*Millions*
1954	804	5.06	1.28	----	6.34
1955	279	1.76	.36	----	2.12
1956	1,773	9.70	2.43	0.02	12.15
1957	635	10.03	3.12	----	13.15
1958	278	3.55	1.25	Trace	4.80
1959	2,232	4.37	8.46	.13	12.96
1960	828	8.00	8.72	Trace	16.72
1961	351	6.05	4.97	----	11.02

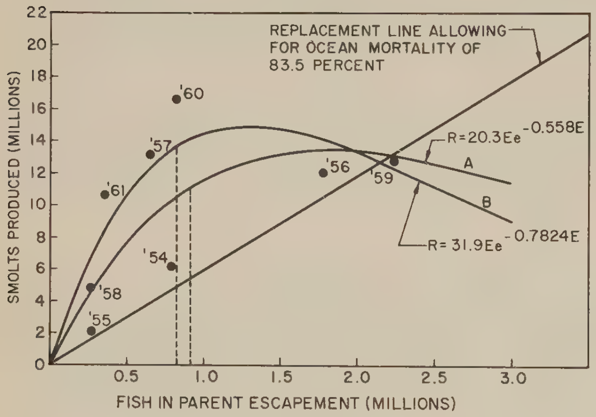

FIGURE 13.—Relations between numbers of smolts produced and number of sockeye salmon in parent escapement in the Naknek system for the escapements in 1954-61. The number beside each point indicates the escapement year. The dashed line indicates the optimum escapement for each curve. R=number of smolts in millions, and E=number in escapement in millions. Curve A fitted to all points; curve B fitted to 1956-61 points (see text).

Ricker-type reproduction curves have been fitted to the smolt-escapement data from the Naknek systems for the escapements of 1954-61 (fig. 13). Curve A was fitted to all points and curve B to the escapements of 1956-61. Smolt production from the 1954 and 1955 escapements may have been underestimated by a substantial amount (because of problems in establishing the procedures for sampling smolts). Curve B is assumed, therefore, to describe the smolt-escapement relation better.

For the Naknek system, estimates of total ocean mortality for sockeye salmon from 3 years of smolt migration ranged from 77.6 to 95.2 percent and averaged 83.5 percent. No attempt was made to correct these estimates for the take of salmon by the high seas fishery.

The replacement line in figure 13 is straight—it is based on the assumption that the average total mortality (83.5 percent) applies to all levels of smolt migrations; i.e., ocean mortality is largely independent of numbers of smolts. If ocean mortality tended to increase with increasing numbers of smolts in the seaward migrations, the replacement line would not be straight but would curve upward. Conversely, if ocean mortality tended to decrease with increasing numbers of smolts, the slope of the replacement line would decrease toward the right. Not enough information is available to determine the nature of ocean mortality, and the safest assumption seems to be that its effects are mostly independent of numbers of smolts entering the ocean.

As indicated in figure 13, maximum yield to the inshore fishery may be realized with escapements ranging from 600,000 to 1 million spawners. If the high-seas catches of Naknek River sockeye salmon were taken into account (i.e., if they were included among the survivors), the total ocean mortality would be lower, the slope of the replacement line correspondingly less, and the apparent optimum escapement range somewhat higher. Thus, we encounter a paradox. If reproduction curves of the kind shown were used to maximize the inshore catch, the total catch (inshore plus high seas) would be less than is biologically possible.

Additional observations are required to define more precisely the form of the smolt-escapement relation and ocean mortality rate.

Ugashik System

Estimates of the numbers of smolts produced in the Ugashik system are available each escapement year, 1956-60 (table 29). These estimates have been used to construct a figure showing the smolt-escapement relation for the system (fig. 14). Escapements of fewer than one-half million fish in 4 of the 5 years caused a crowding of points at the lower end of the scale; interpretation of the form of the smolt-escapement relation is, accordingly, difficult. Smolt production appears nevertheless to increase as the size of the escapement increases. The greatest number of smolts (31.6 million) was produced by the greatest number of adults—2.3 million spawners in 1960. Because we lack observations on escapements of intermediate size, the best that can be determined is that target escapements for the

TABLE 29.—*Number of sockeye salmon in each escapement and number of smolts produced, by year of spawning, Ugashik system, 1956-60*

Year of spawning	Fish in escapement	Smolts			
		Age I	Age II	Age III	Total
	Thousands	*Millions*	*Millions*	*Millions*	*Millions*
1956	425	11.43	0.37	0.06	11.86
1957	215	2.52	2.16	Trace	4.68
1958	280	3.28	3.03	----	6.31
1959	219	.78	3.22	Trace	4.00
1960	2,294	13.47	18.12	(1)	31.59

(1) Age III smolts will migrate seaward in the spring of 1964.

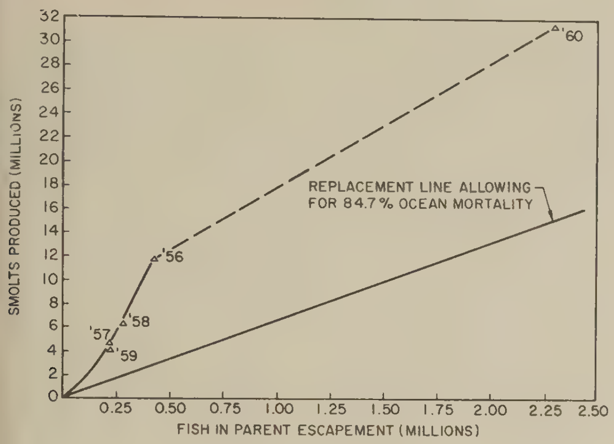

FIGURE 14.—Relation between numbers of smolts produced and number of sockeye salmon in parent escapement in the Ugashik system for the escapements of 1956-60. The number beside each point indicates the escapement year. A broken line is used to connect the values for 1956 and 1960 because the escapements were so different that the probable shape of the curve between them is not apparent.

Ugashik system should probably be greater than one-half million.

Karluk System

Estimates have been made of the numbers of sockeye salmon smolts produced by the Karluk River system for 3 years (1961-63). About 1.5 million smolts were produced each year, although parent escapements varied from 210,000 to 435,000. Within this range of escapements, the relation between numbers of smolts produced and numbers of parents is not definable.

RELATION BETWEEN LENGTH OF SMOLTS AND NUMBERS OF ADULTS IN PARENT ESCAPEMENT

Small smolts would be expected to have greater ocean mortality than large smolts. Indeed, Ricker's (1962) compilation and analysis of return-per-smolt data from six sockeye salmon systems outside Bristol Bay confirmed this general relation. Burgner (1962) determined that a group of age I smolts that migrated from Wood River in 1955 at an average length of about 72 mm. suffered about twice the ocean mortality of a group of age I smolts 90 mm. long that migrated in the same year. This influence of size on survival agrees well with the data shown in Ricker's figure 1 (1962). We, therefore, consider the relation of length of smolts to numbers of adults in the parent escapement and discuss the effects of size of smolts on their survival in the ocean.

Wood System

The relation between the mean length of age I smolts and numbers of adults in the parent escapements in the Wood system is presented in figure 15, where a regression line has been fitted. The equation for the regression of length of age I smolts on number of spawners in the parent escapement is

$$L_I = 87.86 - 4.4X$$

where L_I is the average fork length in millimeters of age I smolts, and X is the parent escapement in millions of spawners. The correlation is significant at the 98-percent level. Thus, the mean length of age I smolts (the dominant age group) is inversely related to the number of parent spawners.

On the basis of this equation, age I smolts from an escapement of 2 million spawners would be expected to have an average length of about 79 mm. and those from 500,000 spawners, about 86 mm.

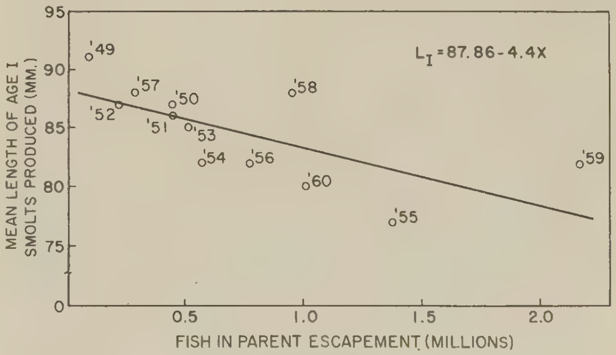

FIGURE 15.—Relation between growth of progeny (as indicated by mean length of age I smolts) and number of adults in the parent escapement, 1949-60, Wood system. The number beside each point indicates the escapement year.

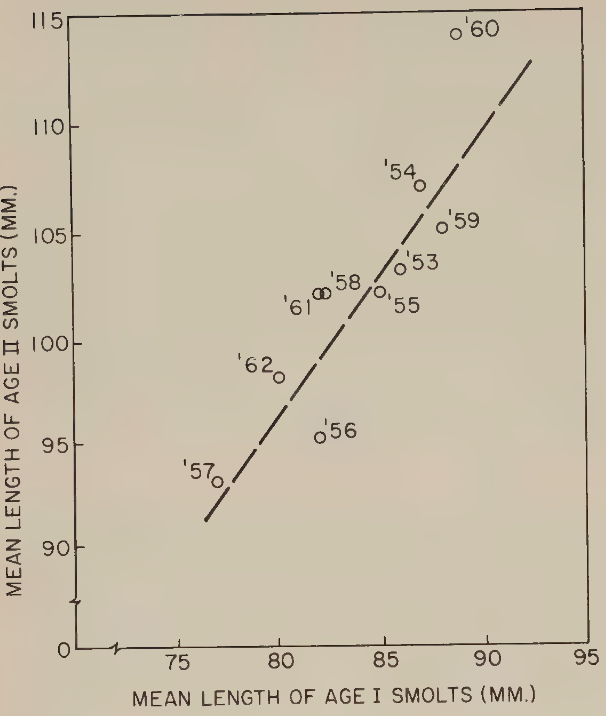

FIGURE 16.—Relation between mean lengths of age II and age I sockeye salmon smolts in the same year of seaward migration, 1953-61, Wood system. The number beside each point indicates the year of smolt migration.

The individual points in the relation between the length of smolts and numbers of adults in the escapement do not fit the regression closely, and, in addition, exact data on natural mortality in the ocean are lacking for the Wood system. Hence, the illustration from the Wood River smolt migration of 1955 given above can only suggest the effect of the size of smolts on ocean survival. It is probable, however, that ocean mortality related to size attained by age I sockeye salmon in fresh water is an important factor in the determination of the numbers of adults in the returns to the Wood system.

The average length of age II smolts was better correlated with the mean length of age I smolts of the following year class than with the number of fish in the parent escapement (fig. 16). This relation suggests the presence of competition for food between age classes of juvenile sockeye salmon.

A lack of significant competition for food among individuals of an age class after their first year in the lake is due to their comparatively small numbers—most sockeye salmon smolts of the Wood River are age I (table 26).

Kvichak System

The data on mean lengths of age I and age II smolts produced by each escapement to the Kvichak system in 1952-60 (table 27) were used to calculate a straight-line regression of smolt length on numbers of adults in the parent escapement for these years. The relation for age I smolts is

$$L_I = 90.64 - 0.7X$$

and for age II smolts

$$L_{II} = 115.51 - 1.4X$$

where L is the length of smolts in millimeters and X is the number of fish (millions) in the parent escapement (fig. 17). The correlation coefficient for age I smolts was $r = -0.73$ and for age II smolts, $r = -0.93$.

The slope of the regression line of smolt size on escapement for age II smolts of the Kvichak system is almost twice that of the age I; the growth retardation caused by competition for food among the progeny of each escapement seems to continue during their second year in fresh water. The contrast to the Wood system in this regard may be the result of the proportionately greater holdover of young to age II smolts in the Kvichak system.

The regression of length of age I smolts on numbers of adults in the parent escapement for the Wood system has a slope six times that derived for age I smolts in the Kvichak system.

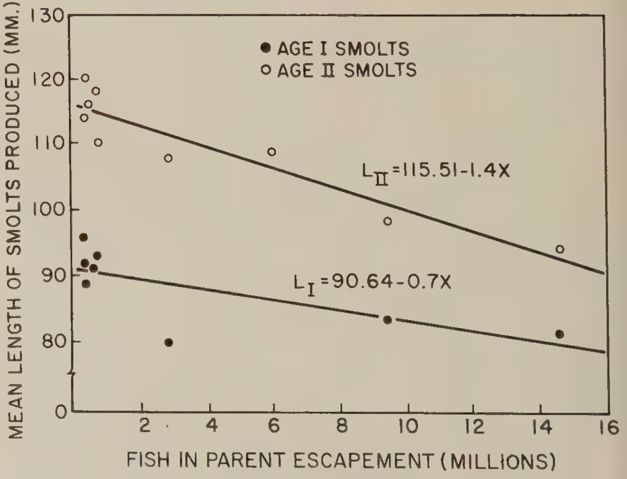

FIGURE 17.—Relation between mean lengths of age I and II sockeye salmon smolts by age class and numbers of adults in the parent escapements, Kvichak system.

This difference may be caused by the relative sizes of the rearing areas of the two systems, because the slopes of the regressions of smolt size on numbers of parent spawners per square kilometer of nursery area are similar for the two systems.

A regression of ocean survival on smolt size with a positive slope of about 0.25 can be calculated from data compiled by Ricker (1962). Thus, although it appears that in the Kvichak system an escapement of about 10 million spawners will produce the greatest number of smolts (age groups I and II combined),[17] the survival of these smolts after they leave the lake will be reduced because the average size of fish in each age group is less than the size of the fewer smolts produced by a smaller escapement. Clearly, the optimum escapement for peak years in the Kvichak system must be determined by maximizing the return as it is influenced by numbers and quality of smolts produced. The optimum escapement must be less, therefore, than that which produces the largest number of smolts.

Another factor also indicates a need for a lower escapement. The regression line in figure 17 has one aberrant point, namely, the length of age I smolts from the 1957 escapement (2,843,000) which followed the large escapement of 1956 (9,443,000). Although the escapement in 1957 was comparatively small, the mean length of age I smolts from the 1957 escapement was less than that of age I smolts from the large 1956 escapement. This discrepancy is interpreted to mean that as young-of-the-year, the age I smolts of the 1957 escapement competed for food with the abundant yearling fish from the 1956 escapement which migrated as age II smolts. Optimum escapement cannot be determined, therefore, by considering one year alone—possible effects of competition between progeny of successive escapements must be carefully considered.

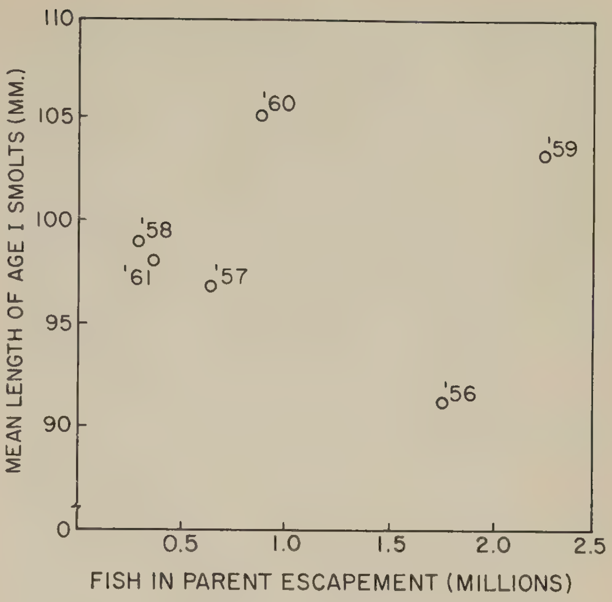

FIGURE 18.—Relation between mean lengths of age I sockeye salmon smolts and number of adults in parent escapements, Naknek system, 1956–61. The number beside each point indicates the parent escapement year.

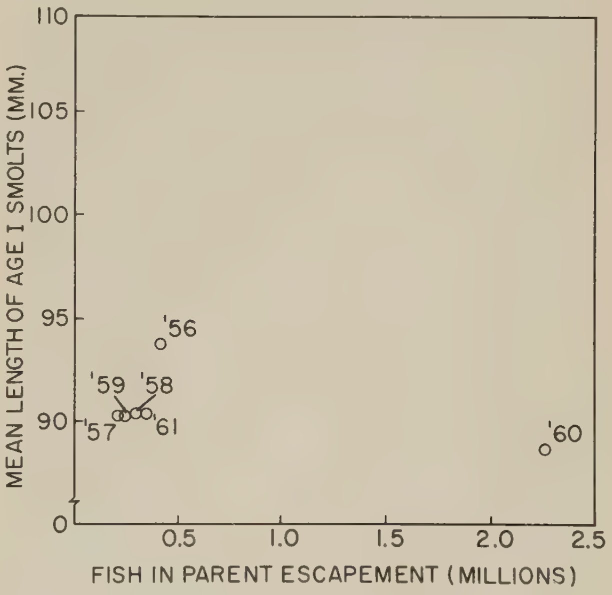

FIGURE 19.—Relation between mean lengths of age I sockeye salmon smolts and number of adults in parent escapements, Ugashik system, 1956-61. The number beside each point indicates the parent escapement year.

Naknek and Ugashik Systems

Little indication exists for the Naknek and Ugashik systems that the average size of age I smolts is correlated with the number of adults in the parent escapement (figs. 18 and 19). The age II smolts show a similar lack of correlation (data not shown). Scales from smolts indicate that the variations in size of age I fish at the time of seaward migration are caused to a great extent by variations in growing conditions in the lakes just before the smolts leave.

Mortality of sockeye salmon in the ocean is influenced by oceanic conditions, the high seas fishery, and the amount of time the salmon spend in the ocean—factors that may mask the effects of the size of smolts on mortality. Estimates of ocean mortality of Bristol Bay sockeye salmon are available for only the Naknek and Ugashik systems (table 30). Age I smolts in the seaward migration from the Naknek system in 1958 were smaller (91 mm.) than smolts of the same age in 1959 (97 mm.) and 1960 (99 mm.). Yet the 1958 group suffered the lowest total ocean mortality (from smolt to return—table 30). Age I smolts of the same year class also had the lowest total ocean mortality for the Ugashik system. The age I smolts in the 1958 Ugashik migration were larger, however, than those of 1959 and 1960. Any effect that smolt size in 1958 might have had on ocean mortality may have been masked by effects of environmental conditions especially conducive to good survival. Valid comparisons can be made only if groups of smolts of different sizes encounter conditions that are similar. Obviously, this situation is rare.

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[17] This estimate is based on data collected through 1963 (see footnote 16).

The data in table 30 afford an opportunity for comparison of ocean mortality for age I and age II smolts. Age II smolts without exception suffered a lower total mortality. How much of this difference can be attributed to their larger size rather than time of entry into the estuary cannot be determined, for age II smolts generally enter the sea at least 1 or 2 weeks before age I smolts.

RELATION BETWEEN FRESH-WATER AGE OF SMOLTS AND NUMBER OF ADULTS IN PARENT ESCAPEMENT

The tendency for slow-growing sockeye salmon juveniles to remain an additional year in fresh water before they migrate seaward has been documented (Foerster, 1937; Barnaby, 1944; Krogius and Krokhin, 1956; Koo, 1962). Data presented by Foerster (1944) suggest that in some studies, however, the tendency is reversed, and slow-growing sockeye salmon go to sea at age I. Also, an increase of a year or more in length of residence in fresh water accompanied an increase in growth rate that resulted from reduction of populations (Krogius, 1961). Little is known regarding the factors that cause juvenile sockeye salmon to migrate to sea.

Wood System

We might anticipate in this system a higher percentage of age II smolts from the larger spawning populations than from the smaller because of the inverse relation between number of parents and growth of progeny during their initial year of lake residence. This tendency is suggested by the data (fig. 20), but the progeny of the large escapement year, 1959, are an outstanding exception to the theory that slowly

TABLE 30.—*Ocean mortality of sockeye salmon by fresh-water age, Naknek and Ugashik systems*

System, year of seaward migration, and fresh-water age	Smolts in seaward migration	Average length	Average time in ocean	Total mortality
	Millions	*Mm.*	*Years*	*Percent*
Naknek system				
1958				
Age I	9.698	91	2.74	82.8
Age II	.362	114	2.25	28.7
Total	10.060	----	2.68	80.8
1959				
Age I	10.035	97	2.88	96.8
Age II	2.431	106	2.99	89.0
Total	12.466	----	2.93	95.2
1960				
Age I	3.553	99	2.64	92.2
Age II	3.118	109	2.56	67.2
Total	[1] 6.691	----	2.57	80.5
1961				
Age I	4.367	103	2.52	85.6
Age II	1.246	113	2.25	50.1
Total	5.613	----	2.39	77.6
Ugashik system				
1958				
Age I	11.438	93	2.17	69.7
Age II	.222	112	2.04	49.7
Total	11.660	----	2.17	69.3
1959				
Age I	2.520	90	2.78	95.4
Age II	.367	120	2.34	75.5
Total	2.887	----	2.59	92.8
1960				
Age I	3.286	90	2.61	95.6
Age II	2.163	108	2.21	81.4
Total	[1] 5.504	----	2.32	90.0
1961				
Age I	.776	90	2.70	93.5
Age II	3.026	112	2.14	85.3
Total	3.802	----	2.20	86.6

[1] The 1960 totals include age III smolts; none were recorded in other years.

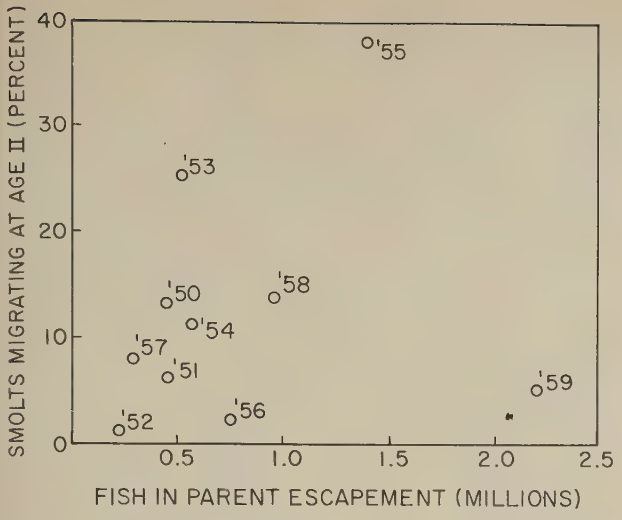

FIGURE 20.—Relation between proportion of total smolt production migrating at age II and number of sockeye salmon in parent escapement, Wood system, 1951-59. The number beside each point indicates the parent escapement year.

growing juveniles go to sea as age II smolts—these progeny grew slowly, but most went to sea at age I. The tow net indices of abundance of this year class as yearlings residing in the lake indicated a considerably higher percentage holdover than was indicated in the index sampling of smolts; some question exists, therefore, as to the accuracy of the index of abundance of age II smolts in the Wood River.

Kvichak System

The lowest recent escapements of sockeye salmon in the Kvichak system (1954 and 1958) produced mostly age I smolts, whereas the intermediate escapements (1953, 1955, 1957, 1959) produced mostly age II smolts. More of the progeny of the largest escapements (1952, 1956, 1960) tended to hold over to age II smolts as the escapement levels increased. The escapement of about 6 million fish in 1952 produced mostly age I smolts (or at least only fish of this age returned n large numbers). The only information we have on the smolt migration in the Kvichak River in 1954 (age I smolts from the 1952 escapement and age II from 1951) is that local residents in Levelock observed it to be "heavy." The 1956 escapement of 9.4 million produced 46 percent age II smolts, and the 1960 escapement of 14.6 million produced at least 78 percent age II smolts (fig. 21, table 27).

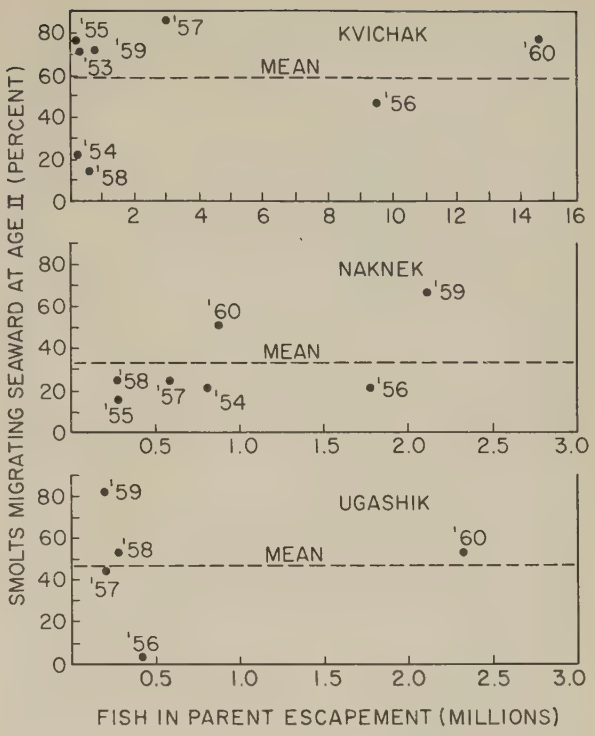

FIGURE 21.—Relation between proportion of progeny migrating as age II smolts and number of sockeye salmon in parent escapement, Kvichak system, 1953–60, Naknek system, 1954-60, and Ugashik system, 1958-60. Figure beside each point indicates year of parent escapement.

Naknek and Ugashik Systems

Data for the Naknek and Ugashik systems do not indicate that the percentage of sockeye salmon progeny migrating seaward as age II smolts is correlated with the number of fish in the parent escapement (fig. 21). The escapements in the Naknek system in 1954-58 ranged from 0.278 to 1.77 million, but the portion of age II smolts remained nearly constant between 16 and 25 percent.

The amount of growth added in the spring before the juveniles migrate as smolts is influenced by climate (Burgner, 1962). In years of favorable growing conditions early in the season, a higher percentage of yearlings may attain some size threshold for migration and leave as age I smolts. Thus, the influence of climate may tend to mask the relation between percentage holdover of progeny in the lakes and the number of parent spawners.

The major sockeye salmon systems on the east side of Bristol Bay tend to have concurrent fluctuations in the percentages of smolts migrating at age II, although the escapement levels vary somewhat independently. The proportions of age II smolts were at or below average for the escapement years 1954, 1956, and 1958 in the Naknek and Kvichak systems and for 1956 and 1958 in the Ugashik system (no data are available for Ugashik in 1954 and 1955). The percentages were above average in the three systems for the escapement years 1959 and 1960 (fig. 21). These concurrent fluctuations suggest the influence of general climatic factors.

RELATION BETWEEN RETURN AND ESCAPEMENT FOR THE NUSHAGAK FISHING DISTRICT

The relation between the numbers of adults returning (catch plus escapement) and the numbers in the parent escapement is of general interest, though frequently the intermediate statistic—numbers of smolts produced—is now available. The longest series of return-escapement data available is for the Nushagak fishing district (Igushik, Snake, Wood, and Nuyakuk Rivers combined) for the escapements of 1946-57 and the resulting returns (table 31).

Table 31.—*Number of sockeye salmon in parent escapements and resulting returns, Nushagak district, 1946-57*

Year of spawning	Fish in parent escapement	Fish in resulting return
	Thousands	*Thousands*
1946	4,719	1,207
1947	2,507	953
1948	2,091	1,484
1949	138	376
1950	573	1,751
1951	540	3,749
1952	434	1,574
1953	829	1,431
1954	692	3,122
1955	1,934	5,056
1956	1,212	2,129
1957	499	520

The return-escapement data from the Nushagak district were used to calculate the recruit-spawner relation (reproductive curves) of Schaefer (1954), Beverton and Holt (1957), and Ricker (1958). When the weighted sums of squared deviations of the observed data from each of the predicted curves were calculated, the deviations were least from the curve derived from Ricker's formula:

$$R = aEe^{-bE}$$

where R = number of sockeye salmon in the return, E = number in the parent escapement, and a and b are constants. For the Nushagak district return-escapement data, a = 3.951 and b = 0.6269. The calculated curve and original data for the Nushagak system are presented in figure 22. The estimated maximum yield is at the point where a line parallel to the replacement line is tangent to the curve—for the Nushagak district this point corresponds to an escapement of about 900,000 fish.

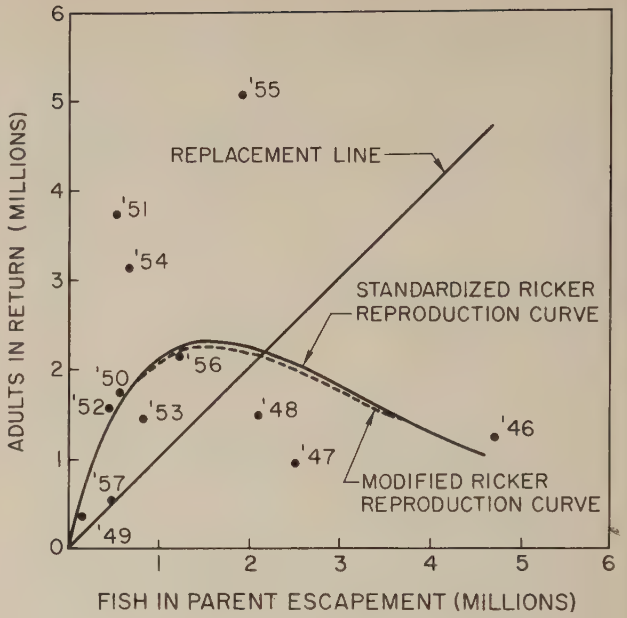

Figure 22.—Relation between number of sockeye salmon in return (catch plus escapement) and number in parent escapement, Nushagak fishing district, 1946-57. The number beside each point indicates the parent escapement year.

Addition of another parameter (n) to Ricker's formula as follows

$$R = aEe^{-bE^{n}}$$

gives greater flexibility in fitting the data. This modified version of Ricker's curve permits more exact fitting of a reproduction curve to observed data.

For the Nushagak data the relation was

$$R = 4.191Ee^{-0.699E^{0.936}}$$

The modification also gives an estimated optimum escapement of about 900,000. This curve is essentially the same as the standardized curve produced by the unmodified Ricker formula.

Ricker's formula can also be used to study the relation of return to potential egg deposition.

The numbers of 2- and 3-ocean female sockeye salmon in the escapements to the Nushagak district are known for 1946-57, and the potential egg deposition by each age group has been estimated (table 32). With potential egg deposition in billions as the independent variable (E), the formula which describes the relation between return and potential egg deposition is

$$R = 1.7456Ee^{-0.2699E}$$

The curves describing this relation permit the estimation of the optimum number of eggs on the spawning grounds. To convert number of eggs to number of spawners, an average fecundity of 4,000 eggs per female and a sex ratio of 1:1 are assumed. This calculation also yields an estimated optimum escapement of about 900,000 fish.

Since 1956 the high seas fishery has taken a substantial portion of the Bristol Bay sockeye salmon run each year. We approximated the high seas catch of fish from the Nushagak fishing district by prorating a portion of the estimated high seas catch of each ocean age group of Bristol Bay sockeye salmon according to the ratio of Nushagak district returns to the total Bristol Bay returns. The optimum escapement was then computed with these corrected returns; it was again found to be between 0.9 and 1.0 million fish.

TABLE 32.—*Number of 2-ocean and 3-ocean females in sockeye salmon escapements and estimated potential egg deposition, Nushagak district, 1946-57*

Year	Two-ocean females [1]		Three-ocean females [1]		Potential egg deposition
	Fish	Eggs	Fish	Eggs	
	Thousands	*Millions*	*Thousands*	*Millions*	*Millions*
1946	2,638	9,600	429	1,840	11,440
1947	850	3,093	704	3,020	6,113
1948	109	397	958	4,110	4,507
1949	32	116	50	215	331
1950	163	593	158	678	1,271
1951	110	400	187	802	1,202
1952	123	448	116	498	946
1953	126	459	338	1,450	1,909
1954	321	1,168	60	257	1,425
1955	836	3,042	228	978	4,020
1956	358	1,303	248	1,064	2,367
1957	115	418	164	704	1,122

[1] The average fecundities of 2- and 3-ocean females are 3,639 and 4,290 eggs on the assumption of mean lengths of 490 and 560 mm., respectively (Mathisen, 1962).

The four reproductive curves, all similar, indicate that an escapement of about 0.9 million sockeye salmon to the Nushagak district will yield the highest surplus of return over parent escapement. Escapements ranging from 0.6 to 1.2 million would theoretically produce about the same surplus because the curve is nearly flat in this area (fig. 22).

A drastic decline in the returns to the Nushagak district occurred in 1946-54. In fact, the returns did not equal the parent escapements in 1946-48. The returns from the relatively large escapements of these 3 years may have been abnormally low. If data from additional years indicate that it is more common for relatively large escapements to produce large returns, the calculated optimum escapement will be higher than 0.9 million.

The escapements of sockeye salmon to the Wood system have averaged about 70 percent of the total for the Nushagak district in recent years; this fact suggests an optimum escapement for the Wood system of about 630,000 sockeye (70 percent of 900,000). The only other period when escapements were counted for the Wood system was in 1908-19, when adults were counted at a weir on Wood River by the U.S. Bureau of Fisheries (no estimates of escapements were made for the other systems of the Nushagak district during these years). Although the average catch in the Nushagak district approached 5 million fish in 1908-19, escapements to the Wood system averaged only 750,000 sockeye salmon (Bower, 1920). The escapements to the Wood system from 1908 to 1919, therefore, averaged only slightly higher than our calculated optimum based on recent data. After 1919, the average catch in the Nushagak district dropped and remained at about 3 million until 1946—we have no satisfactory explanation for the higher production in 1908-19.

INTERPRETATION OF FINDINGS AND APPLICATION TO MANAGEMENT

In this final section we consider those characteristics of the sockeye salmon populations, the spawning grounds, and the nursery lakes that bear on carrying capacity and optimum escapement and, finally, give our best estimate of the optimum escapement for each system. The Mainland Systems tributary to Nushagak Bay—Igushik, Snake, Wood, and Nuyakuk—are discussed together. The Kvichak system of the Mainland group and the Peninsula Systems are discussed individually. The Alagnak and Egegik systems are not discussed.

Igushik, Snake, Wood, and Nuyakuk Systems

The Igushik, Snake, Wood, and Nuyakuk systems are all tributary to Nushagak Bay, the source of most of the fish taken in the Nushagak fishing district. These systems have a combined area of 867 km.^{2} distributed as follows: Igushik system, two lakes and 74 km.^{2}; Snake system, one lake and 89 km.^{2}; Wood system, five main lakes and 425 km.^{2}; and Nuyakuk system, three lakes and 279 km.^{2} The Nushagak fishery operates on a mixture of stocks from the four systems, and the catch for the district is assigned to each system on the basis of age composition and escapement levels. Therefore, the several systems of the district are evaluated in part as a unit.

In the early 1900's the annual commercial catch of sockeye salmon in the Nushagak district averaged about 5 million fish. It declined to an annual average of about 3 million in 1920-45 and suffered another marked decline in the next 10 years. Since 1955 the annual catch has been generally increasing but has not yet reached the pre-1945 levels.

The recent annual escapements to systems of Nushagak Bay have been distributed about as follows: Wood system, 70 percent; Igushik system, 23 percent; Nuyakuk system, 5 percent; and the Snake and several minor systems, 2 percent. The Nuyakuk and Snake systems historically may have produced at much higher levels.

Because of the selective action of the commercial fishery (larger fish are more susceptible to capture, and the time and route of migration and, therefore, exposure to the fishery may vary among the stocks), fishing mortality has not been uniform among the stocks in the Nushagak district. In 1948-60 the percentages of the large 3-ocean adults returning to the Wood, Igushik, and Nuyakuk systems were about 30, 60, and 70 percent, respectively (from data compiled by Burgner, footnote 7).

Studies of migration routes and timing of adult sockeye salmon in Nushagak Bay have shown that runs to the Wood and Igushik systems are partially segregated in the fishing areas (unpublished data of the Bureau of Commercial Fisheries Biological Laboratory, Auke Bay, Alaska). There is evidence that in the past, runs to the Igushik system may have been subject to lower fishing intensity than those from the Wood system. Were the intensity of fishing the same on the two runs, a higher percentage of the fish going to the Igushik system would be captured because of the predominance of the 3-ocean fish.

Since sockeye salmon in the escapement to the Nuyakuk system are primarily 3-ocean fish, and this run of larger fish is presumably fished as intensively as the run of smaller fish in the Wood system, the run to the Nuyakuk system probably suffers a consistently heavier fishing mortality than the run to the Wood system. Over the years this heavier mortality could have caused a decline in the relative contribution of the Nuyakuk system to the Nushagak fishery.

Certain spawning areas within the Wood system consistently contain more 3-ocean than 2-ocean fish. Thus, fishing mortality may vary between groups within a system as well as between systems.

Estimates of the capacities of the potential spawning areas in each system in the Nushagak district indicate that the potential area greatly exceeds that used at the current levels of escapement.

The factors that limit production of juvenile sockeye salmon in systems tributary to Nushagak Bay appear to lie in the rearing areas of the lakes rather than in the spawning areas. Our studies of the limnology of the lakes of these Mainland Systems indicate that they are generally poorer in minerals than lakes of the Peninsula Systems and have a higher calcium-to-sodium ratio. The watersheds in Nushagak Bay have mostly sedimentary rocks, which contribute smaller amounts of minerals to the lake waters than do the igneous rocks common in the watersheds on the peninsula—an area of recent volcanism. Lakes of the Igushik and Wood systems nevertheless ranked fairly high in primary productivity. Lakes in the Nuyakuk system had the highest mineral content of lakes tested in the Nushagak district, but rates of carbon fixation were low. Lakes of the Nushagak Bay area have less of an oceanic climate than the other lakes studied—ice covers the lakes longer, and thermal stratification during the summer is more pronounced.

Although the four main lakes in the Wood system have similar limnological characteristics and similar numbers of sockeye salmon per square kilometer of lake in the escapements, they contrast sharply in the proportion of kinds of spawning grounds. The similarities in numbers per unit of lake area in the average escapements indicate that the population level is controlled by the capacity of the nursery areas in each lake.

The production of juvenile sockeye salmon in the lakes of the Wood system increases linearly as the escapement increases, up to a density of 5,000 spawners per square kilometer of lake. Above this density the relation is no longer linear, and the production of juveniles per spawner declines when escapements exceed 6,000 per square kilometer. To have 5,000 spawners per square kilometer in all lakes of the system would require an escapement of 2,125,000 fish. At this density, however, the growth of juvenile salmon is considerably reduced. The mean length of age 0 fish in September is inversely related to the size of the parent escapement in each of the lakes of the Wood system. The mean length of age I smolts leaving the system also is inversely related to numbers in the parent escapement.

The combined effect of large populations of juveniles is to increase total mortality (freshwater and ocean) by causing many juveniles to remain an extra year in fresh water and to be of smaller average size for their age when they reach the ocean. This increase in mortality tends to make the population self limiting.

Threespine sticklebacks and Arctic char are the species of fish thought to have the most important effects on juvenile sockeye salmon in the Igushik, Snake, and Wood systems. In the Wood system, threespine sticklebacks and juvenile salmon use the same food supply, and, therefore, the growth of sticklebacks and age I salmon is reduced when large numbers of age 0 salmon are present. In all three systems Arctic char is the chief predator on small fish and probably eats substantial numbers of sticklebacks and juvenile salmon. The role of sticklebacks as a competitor for food and as a buffer between Arctic char and sockeye salmon and the effect of the Arctic char in keeping stickleback populations in check are not understood.

The recent average escapement of sockeye salmon per unit area of lake has been higher in the Igushik than in the Wood system. Juveniles from the larger escapements in the Igushik system have not grown as well (the smolts have not been as long) as those from the smaller escapements, so that here also the food supply apparently limits growth. Preliminary limnological studies show no marked difference in richness between the waters of the Igushik and Wood Lakes, and the greater concentration of spawners in the Igushik system appears to be caused by differences in the intensity of fishing on the two stocks.

Although primary productivity is low in the Nuyakuk system, escapement densities are probably too low to produce enough juvenile salmon to tax the food supply. Spawning areas appear to be far in excess of the present need. Relatively heavy fishing pressure probably has contributed to the present low level of the runs. Lake trout are more plentiful than Arctic char in the Nuyakuk system; the lake trout may be the primary predator on young salmon and sticklebacks.

The return-escapement relations of sockeye salmon in the Nushagak district in 1946-62 indicate that the optimum escapement is about 1 million fish, but that escapements between 600,000 and 1.2 million will produce near-optimum results.

If spawners were properly distributed, production in the Nushagak fishery could probably be increased by increasing the escapements. In an escapement of 1 million, for instance, if 70 percent of the fish went to the Wood system the lakes of the system would have an average density of 1,650 spawners per square kilometer. If distribution of spawners among the lakes were even, this density could be profitably exceeded. In years of uneven distribution of spawners, escapements should be held at a lower level to avoid overstocking of some rearing areas. Further, the mesh size of the gill nets used in the fishery could be regulated so as to obtain escapements of the two primary ocean-age groups in proportions that would more fully use all of the lakes of the Wood system and would give more protection to the populations of the Nuyakuk system. All the consequences of changes in the size of the mesh must be carefully studied, however, before this change is initiated.

Kvichak System

The Kvichak, the largest sockeye salmon system in Alaska, consists principally of two lakes, Iliamna and Clark, which total 2,889 km.^{2} The sizes of the runs in this system are cyclic. The range of the escapement in 1955-63 was 250,000 to 14.6 million. In 1931-61 the annual catch of the Naknek-Kvichak fishery averaged about 7.5 million fish. During the years of very large returns the Bristol Bay catch is dominated by salmon returning to the Kvichak system.

Within the Kvichak system there are many spawning groups of sockeye salmon. Adult fish of the different spawning groups are not segregated by time of passage into Iliamna Lake. The returnees generally have spent 1 or 2 years in fresh water and 2 or 3 years in the ocean; four principal age groups result. The age composition of the adults differs among the spawning grounds. In 1962, streams, with one major exception, contained significantly higher proportions of 2-ocean spawners than did beaches. It is not known if the relative proportion of 2- and 3-ocean fish is genetic. Fresh-water age, however, is probably determined more by the environment than by genetic factors.

Sockeye salmon generally spawn within the Kvichak system from early August to mid-October—a time span that probably reflects the adaptation of the various spawning populations to the different types of environments. Fry also emerge over an extended period. An indirect measure of the relative time of emergence is the size of juveniles during their first summer. The greatest range in time of emergence in the Kvichak system is in Lake Clark, where age 0 sockeye salmon in August range from 32 to more than 60 mm.

Although estimates of the amount of potential spawning area in the Kvichak system are incomplete, the available data indicate that the carrying capacity for this system is about 20.5 million spawners. Even the largest recorded escapement —14.6 million spawners in 1960—did not approach this figure (footnote 10). Between 1955 and 1963, the escapements in terms of number of adults per square kilometer of lake ranged from 84 in 1955 to 11,890 in 1960. The escapements to Lake Clark have not been well documented but are thought to be somewhat less than 10 percent of the total for the Kvichak system.

The greatest abundance of age 0 sockeye salmon in Iliamna Lake is in the vicinity of the heaviest spawning—in the east half of the lake. As the age and size of young fish increase they spread over the whole lake, and the largest fish are found in the western part.

Our knowledge of predators and potential food competitors in the Kvichak system is scanty. We do know that the distribution of threespine sticklebacks, the main potential competitor with juvenile sockeye salmon for food, is similar to that of age 0 salmon. Large populations of lake trout, Dolly Varden, Arctic char, and rainbow trout are also present. We suspect that competition for food and predation are important factors in the production of juvenile sockeye salmon in Iliamna Lake. The effect of predation would be much heavier in years of low abundance of juveniles and, thus, would tend to maintain the cyclic pattern of the Kvichak run.

Lakes of the Kvichak system are generally similar limnologically to lakes of the other Mainland Systems. The values for pH and concentrations of total dissolved solids and total alkalinity are intermediate among all systems. The rates of carbon fixation in Iliamna Lake were near the lower end of the range for mainland lakes, but in Lake Clark the rates were much reduced, probably because of the opacity of the water. The Kvichak system ranks in the same general position in numbers of spawners per lake area and in rate of carbon fixation per square meter, i.e., in the low range of the intermediate values.

Limnological studies in the Kvichak system span too short a time to permit comparisons between years. Future studies will determine whether dissolved minerals differ between off and peak years of the cycle; such differences could cause cyclic manifestations or, conversely, be caused by them.

Observations span too few years to indicate the relation between production of fry and parent escapement.

The relation between production of smolts and parent escapement varies, depending on whether we consider peak years or low years. The progeny of the 2 peak years studied, 1956 and 1960, had production indices of smolts of 181 and 150, respectively, although the escapement was almost 50 percent greater in 1960 than 1956. In both years, 2-ocean fish were dominant in the escapement—98 percent in 1956 and 99 percent in 1960. The maximum number of smolts is apparently produced at escapements below the 1960 level of 14.6 million (based on data collected through 1963). A reproduction curve based on the data of the 2 peak years 1956 and 1960 indicates that a range of escapements of 5 to 12 million will not drastically change the number of smolts produced.

A target escapement for peak years must be based on several factors in addition to the number of smolts produced. The data clearly show a negative linear relation between the average length of smolts produced and the escapement level—that is, growth is retarded through intraspecific competition for food when the population of juvenile salmon is too great. It is known that ocean survival is generally positively correlated with size of smolts at migration, although data do not exist to calculate the differences in survival rates for the Kvichak system.

Whether the progeny of large escapements migrate at age I or age II in the Kvichak system is probably determined by the size they attain during their first year in fresh water. The percentage of young salmon that migrate as age II increases as the population of young salmon in the nursery areas increases, although the percentage holdover to age II can be modified by the environment. Any extension of the average length of the fresh-water life in the Kvichak system will also extend the length of the reproductive cycle.

In assessing the optimum escapement for the Kvichak system, we must consider production in an entire cycle and not for just one outstanding year such as 1956. Before 1942, the returns of the peak years contained progeny of at least two (and usually three) escapements.

If we accept the thesis that the carrying capacity of the nursery areas limits the production of sockeye salmon in the Kvichak system, a rational approach to regulation would be to utilize the nursery areas to the fullest every year. This approach would require the presence of age I juveniles (fish that will migrate as age II smolts) in addition to the young-of-the-year, because only age I and older fish use the larger downlake portion of the nursery area. Historically, fish that went to the ocean as age II smolts made up almost 60 percent of the catches in the Naknek-Kvichak district (fish from the Kvichak system constituted the greater share of the catch in peak years).

If we also assume that the historical sequence of large and small escapements of the Kvichak cycle is the one which will yield the greatest return over many years, the following conclusion is unavoidable. The Kvichak system must be managed so as to provide at least two, and preferably three, successive large escapements preceded and followed by smaller escapements. The relative abundance of fish in the successive years of large escapements may be manipulated in such a manner as to provide about the same potential egg deposition each year. Because of the present conditions of the stocks, it may take two or more cycles to reestablish this pattern. Only after the historical pattern has been restored will it be possible to define an optimum escapement for the peak years, which may well be higher than that desirable during the present transition period.

Collection of vital statistics must be improved substantially to define the optimum escapement of sockeye salmon for the Kvichak system. To clarify the known vagaries of cycles of abundance and reproductive capacity, not only must better methods be devised to assess the escapement, the standing crop of young salmon in the lakes, and the smolt migration but many other factors must be evaluated.

Naknek System

The Naknek system consists of a series of interconnected lakes totaling 790 km.^{2} Drainage to Bristol Bay is via the Naknek River into the Naknek-Kvichak fishing district. Adult sockeye salmon returning to the Naknek system mingle in the fishing area in Bristol Bay with others bound for the Kvichak and Alagnak systems. Catches were reported for the Naknek-Kvichak district as a whole until recent years, when portions of the catch were assigned to the respective river systems of the district on the basis of age composition and escapement. Since 1957 the run to the Naknek River has averaged 1.6 million fish—the commercial catch averaged 760,000 and the escapement 840,000.

The escapement of sockeye salmon to the Naknek system is composed mainly of 2- and 3-ocean fish, the relative strength of the groups varies widely from year to year. Fresh-water and ocean ages and numerical strength of the various spawning units within the system fluctuate somewhat independently of each other. The various spawning units seem to pass through the trunk river at about the same time.

Estimates of the total capacity of the potential spawning areas of the system are in excess of the average escapement for the past 10 years. Only limited data are available on the escapement of sockeye salmon per unit lake area for each lake, but great variations are known to exist among the lakes of the system. In 1961 Coville Lake received 6,600 spawners per square kilometer of lake. This density of spawners produced a catch of 150 age 0 fish per tow in 1962. North Arm had a spawner density of 55 per square kilometer of lake in 1961 and a catch of age 0 fish of 0.5 per tow in 1962. Migration of presmolt juveniles, however, results in the accumulation of young in the rearing areas of Naknek Lake regardless of the distribution of spawners. The studies have run too few years to determine the relation between the abundance of age 0 fish and various levels of the parent population.

The abundance and growth of juvenile sockeye salmon and other species and the primary productivity of the lakes varied between years and among the lakes. Differences in primary productivity between years were accompanied by marked differences in growth of juvenile sockeye salmon, independent of their abundance. The abundance of juveniles was greater in 1962 than in 1961, but the rate of growth was greater in 1962. The primary productivity, on the other hand, was greater in 1962 than in 1961 because of differences in climate. The species and abundance of fish associated with the juvenile sockeye salmon vary among the lakes and among areas within the lakes. Threespine sticklebacks were universally present, and their abundance was matched only by pond smelt in Lake Coville and pygmy whitefish in Brooks Lake. The areas of the Naknek system that yielded the largest catches of juvenile sockeye salmon or the fastest growing juveniles also yielded the largest catches of associated species. The role of the associated species as competitors or predators, or as buffers between predators and juvenile sockeye salmon, is unknown. Several potentially important predator fish are present in the Naknek system, but their significance is not known.

Lakes of the Naknek system have limnological characteristics that fall between those that are characteristic of lakes of the Mainland Systems and also the other lakes of the Peninsula Systems. Lakes of the Naknek system are richer than the mainland lakes in total dissolved solids, total alkalinity, sodium, silica, iron, and manganese and generally richer in many of the other items measured. The large quantities of igneous materials in the watershed and wind-borne materials from the ocean apparently contribute substantially to this richness. These lakes are influenced by the oceanic climate; their ice covers break up relatively early in the spring. Thermal stratification is seldom pronounced, and strong wind action mixes surface waters with deeper waters from time to time during the summer. Rates of carbon fixation by photosynthesis are relatively high, and the standing crops of phytoplankton are similar to those of other peninsula lakes. Because of differences in drainage and basin types, lakes in the Naknek system nearly encompass the range of types of sockeye salmon nursery lakes along the Alaska Peninsula, although Chignik and Black Lakes rank higher than any Naknek lakes in photosynthetic rates and chlorophyll values.

Data on the relation of smolt production to escapement in the Naknek system in 1954-60 show an increase in numbers of smolts produced with increased escapement up to about 1 million fish. Accurate determination of optimum escapement from reproduction curves based on smolt-escapement relations is dependent on knowledge of mortality rates in the ocean. For the Naknek system, estimates of total ocean mortality for sockeye salmon from 3 years of smolt migration ranged from 77.6 percent to 95.2 percent and averaged 83.5 percent (no correction for a high seas fishery).

If total ocean mortalities range around 83.5 percent, maximum yields may be realized with escapements of 0.6 to 1.0 million. The presently known spawning areas have a capacity of about 1.3 million spawners. Escapement levels do not appear to have any effect on the size of age I smolts or the percentage of the progeny that migrates seaward as age II smolts. The Naknek lakes are richer in basic nutrients and generally have higher rates of phytoplankton production than the mainland lakes. Major differences in climate between years probably influence the growth of young sockeye salmon more strongly than do differences in their density. At present we do not know whether the upper limit on the production of smolts is imposed by the capacities of the spawning areas, the capacities of the nursery areas, or a combination of several factors that may or may not include these two.

Ugashik System

The Ugashik system on the Alaska Peninsula is the southernmost of the major river systems that drain into Bristol Bay. The system consists of two lakes, Upper and Lower Ugashik, which total 385 km.[2] Our studies in the Ugashik system included limnological observations, continuation of studies of smolts, catch, and escapement, and analysis of data previously collected.

Commercial fishing began in the Ugashik district in 1889 when several small salteries were established. Unlike the other districts of Bristol Bay, the Ugashik fishery developed rapidly and experienced a decline in the catch several years before peak production was achieved in the Egegik and Naknek-Kvichak districts.

The Ugashik also differs from the other Bristol Bay systems in that it has had several periods of peak production of sockeye salmon. The first was early—from 1899 to 1903—when the annual catch averaged 1,114,400 fish. A period of gradual decline followed, and in 1911 the catch reached its lowest point—about 113,000 fish. Between 1904 and 1916 the annual catch averaged 368,400; from 1917 to 1923, it rose to about 882,000. The 1924-42 period was characterized by generally low catches. A regulatory closure of the fishery occurred in 1935. Fishing effort in the district was greatly curtailed in 1940 and 1941 because of the war. Annual catches in 1942-48 averaged nearly 1 million fish. Since 1949, with a few exceptions (1953, 1954, and 1960) the annual catch has averaged less than 500,000.

Escapement counts were obtained for the Ugashik system in 1925-32 and 1949-63. Escapements during the earlier period ranged from 149,000 in 1929 to 1,380,000 in 1931 and averaged about 533,000 fish; escapements in the later period varied from 77,000 to 2,294,000 and averaged about 574,000.

The Ugashik system, in common with other Peninsula Systems, is currently supporting escapement densities that average about 1,300 sockeye salmon per square kilometer of lake. This density is about one-sixth of that observed in the Chignik and Karluk systems and about one-half of that of the Wood system. Most of the sockeye salmon of the Ugashik system spawn in tributary streams that drain the foothills of the Aleutian Range.

Limnological observations, though not as extensive as those made in other systems, indicate that the Ugashik lakes rank low in total dissolved solids, phytoplankton abundance, and primary productivity.

Estimates of the numbers, ages, and sizes of smolts have been obtained annually since 1958. We cannot see a relation between the size of smolts and parent escapement nor between the proportions of each year's progeny that migrate seaward at age II and escapement. It is possible that relationships are masked by year-to-year variations in environmental conditions.

Although the size of smolts in the Ugashik system apparently is not related to escapement, the number of smolts produced is. The greatest recorded escapement (2.3 million fish in 1960) produced the greatest recorded smolt migration (31.40 million). Low escapements of 215,000 in 1957 and 219,000 in 1959 resulted in 4.33 million and 4.08 million smolts, respectively. The escapement of 425,000 fish in 1956 produced about 12 million smolts. Because no escapements have been of intermediate size, it is not possible to define precisely the smolt-escapement relation over the entire range. All that can be determined now is that smolt production increases markedly with increasing escapement up to about one-half million. The results from the large 1960 escapement show only that increases in numbers of smolts can be realized from escapements greater than one-half million.

The best that can be inferred from the suggested form of the smolt-escapement relation is that the target escapement should be at least 500,000.

Chignik System

The history of the fishery on sockeye salmon runs of the Chignik system is similar to that of the Nushagak district in that the catch remained high until the 1920's, then dropped to a lower level from which it has never recovered.

The two lakes in the Chignik system—Black and Chignik—have dissimilar physical characteristics. Black Lake (mean depth, 3 m.) is the shallowest of the lakes we studied. Chignik Lake has less area than Black Lake but has six times the volume. The total area of the two lakes is 61 km.^{2}

Chignik Lake supports an unusually large escapement of sockeye salmon per unit lake area. The average escapement of 14,000 per square kilometer of lake for 1955-62 is the highest for the lakes studied. Black Lake had an average escapement of about 4,600 per square kilometer over the same period.

Chignik and Black Lakes had the highest primary productivity and chlorophyll *a* concentrations of the lakes studied. The richness of the lakes is undoubtedly the main reason that the

Chignik system has been able to produce large numbers of sockeye salmon per unit lake area.

Although spawning in the Chignik system is primarily in streams, about one-third of the spawning in Chignik Lake is on the beaches. Most of the stream spawning is in the longer streams. No estimates have been made of potential spawning area, but the level of sockeye salmon production by the Chignik system does not appear to be controlled by the capacity of the spawning grounds.

The runs to Black and Chignik Lakes are segregated in time of passage through the fishery. This segregation is significant because it permits control of the escapement to each lake by regulation of the fishery.

The adults returning to the Chignik system are predominantly 3-ocean fish.

The average time juvenile sockeye salmon remain in fresh water is different in the two lakes; the smolts from Black Lake are mostly age I, and those from Chignik Lake are mostly age II.

Age 0 sockeye salmon are reared in three major areas in the Chignik system—Black Lake, Chignik Lake, and Chignik Lagoon. Most of the juvenile sockeye salmon that originate in Black Lake remain there to the smolt stage, although some age 0 fish migrate into Chignik Lake. The brackish water of Chignik Lagoon is the rearing area for a significant part of the Chignik Lake progeny.

The growth of juvenile sockeye salmon is inversely related to the density of the parent population within each of the two lakes. Accurate indexing of the abundance of migrating smolts has not been achieved in the Chignik system, but studies of the size and age composition of the smolts and of abundance and growth of juveniles in the lakes are in agreement. Both studies indicate an increase in abundance, a reduction in growth rate, and an increase in average length of fresh-water residence for progeny of larger escapements. Also, the density of spawners is generally lower, and the juveniles grow faster in Black Lake than in Chignik Lake.

The juvenile sockeye salmon produced by the Chignik system are larger than those of the Wood system at comparable parent population densities—an indication that growing conditions are more favorable in the Chignik system.

Several species of fish other than sockeye salmon are also present in the system. Threespine and ninespine sticklebacks and pond smelt are present and are potential competitors of sockeye salmon for food; they also may act as buffer species between sockeye salmon and predators. The potential competitors are much more abundant in Black than in Chignik Lake; possibly they are held in check in Chignik Lake by the great abundance of young sockeye salmon. Young coho salmon and Dolly Varden, also present, are the system's principal predators on juvenile sockeye salmon. Arctic char and lake trout are not present.

The abundance of associated species and the growth of juvenile sockeye salmon indicate that recent escapements in the Chignik system as a whole have been adequate, but apportionment of the escapement to the two lakes must be considered. Low escapements to Black Lake and the resultant underutilization of its nursery areas by juvenile sockeye salmon may be one reason for the large populations of potential competitors in this lake. In contrast, the relatively high escapements to Chignik Lake have resulted in a shortage of food that has undoubtedly led to the reduced growth and survival of juvenile sockeye salmon and perhaps kept the populations of potential competitors low. The optimum escapement to Black Lake, therefore, is greater than the present level of escapement; to Chignik Lake it is considerably less than the larger escapements of recent years.

Suggested target escapements for each lake are based on the relative success of recent escapements and the effective rearing areas of the lakes. Although the total area of Black Lake is 39 km.^{2}, the effective rearing area is only about 30 km.^{2} because of extensive shoals not utilized by juvenile salmon. We recommend that escapements to Black Lake should be increased from the recent average of 4,600 per square kilometer of effective rearing area to 6,000 to 8,000, or a total of 180,000 to 240,000 fish.[18] The effective rearing area of Chignik Lake as determined from tow net catches includes the entire surface area of 22 km.^{2} The suggested escapement to Chignik Lake is 8,000 to 10,000 per square kilometer or a total of 180,000 to 220,000 fish. This escapement is a reduction from the average in recent years of 14,000 adults per square kilometer.

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[18] Recent studies of distribution and growth of species which compete with juvenile sockeye salmon for food and space in the Chignik system suggest that the populations of competitors would be reduced by larger populations of juvenile salmon. Therefore, the attainment of the recommended escapements might make it possible to increase escapements considerably above 240,000.

Karluk System

The Karluk River sockeye salmon run has been historically among the more valuable in Alaska. Commercial fishing began at Karluk in 1882. Several million fish were harvested annually in the early years of the fishery (1885-95), but a long-term decline began after the turn of the century. This declining trend continued in spite of attempts to maintain escapement levels; in recent years, the total run seldom has exceeded 1 million fish.

The timing of the run of adult sockeye salmon to the Karluk system is similar to that of the Chignik system in that it extends 4 to 5 months. The Karluk run has late spring and fall peaks. Beach spawning is insignificant in most years, and most of the spawners are dispersed over the lateral and terminal tributaries and the outlet, Karluk River. Occasionally, however, as much as 25 percent of the escapement may use beach areas. Certain terminal streams and beach areas are used by both spring and fall spawners. The lateral tributaries, however, are used almost exclusively by spring spawners.

The individual spawning areas in the Karluk system are occupied continuously for about 5 weeks to 5 months by a succession of spawners, with the result that many more spawners are accommodated than could be if they all spawned in 2 or 3 weeks. This occupation by successive waves of spawners introduces questions as to the effect of superimposition of redd sites on the success of spawning. We do not know the answers.

The Karluk Lake watershed is composed of sedimentary rock and is so situated as to be strongly influenced by the oceanic climate. The lake waters originate from snowmelt and surface runoff. Two small lakes, Thumb and O'Malley, drain into separate arms of Karluk Lake.

The concentrations of most of the chemical constituents in Karluk Lake are similar to those of lakes of the Alaska Peninsula, particularly the high concentration of sodium and the low levels of nitrate nitrogen and total alkalinity. Of all the lakes studied, however, Karluk Lake is second only to those of the Chignik system in productivity as measured by rate of carbon fixation and content of chlorophyll *a*. The very high productivity is paralleled by the rank of the Karluk system as first in density of spawners per unit lake area.

The growth of juvenile sockeye salmon was correlated positively with changes in lake productivity and negatively with the abundance of juveniles in 1961 and 1962. Because of varying numerical strength of young from a protracted period of fry emergence and migration, growth data are difficult to interpret.

The only abundant potential competitor with juvenile sockeye salmon for food in Karluk Lake is the threespine stickleback. Arctic char and Dolly Varden are the most abundant predators.

The estimate of numbers of smolts produced in Karluk Lake each year in 1961-63 was about 1.5 million. Numbers of smolts and numbers of adults in the parent escapements were not related; the parent escapements ranged from 210,000 to 435,000 fish.

Data on fluctuations in abundance of sockeye salmon in Karluk Lake have been analyzed in some detail by Barnaby (1944) and Rounsefell (1958). Portions of these data that deal specifically with the return-escapement relation have been reported in a bulletin of the International North Pacific Fisheries Commission (1962), where it is concluded that in the past, escapements of about 750,000 fish have produced the largest surplus of return over escapement. The expanded research in 1961 and 1962 did not yield new information that would alter this conclusion. Recent work serves, however, to emphasize that restoration of the Karluk runs to former high levels will require considerably more than mere manipulation of numbers of spawners in the escapement. Evidence suggests that the average reproductive capacity of the sockeye salmon in the Karluk system was reduced while the run was in decline. Current research at Karluk is directed toward determination of the cause of this reduction.

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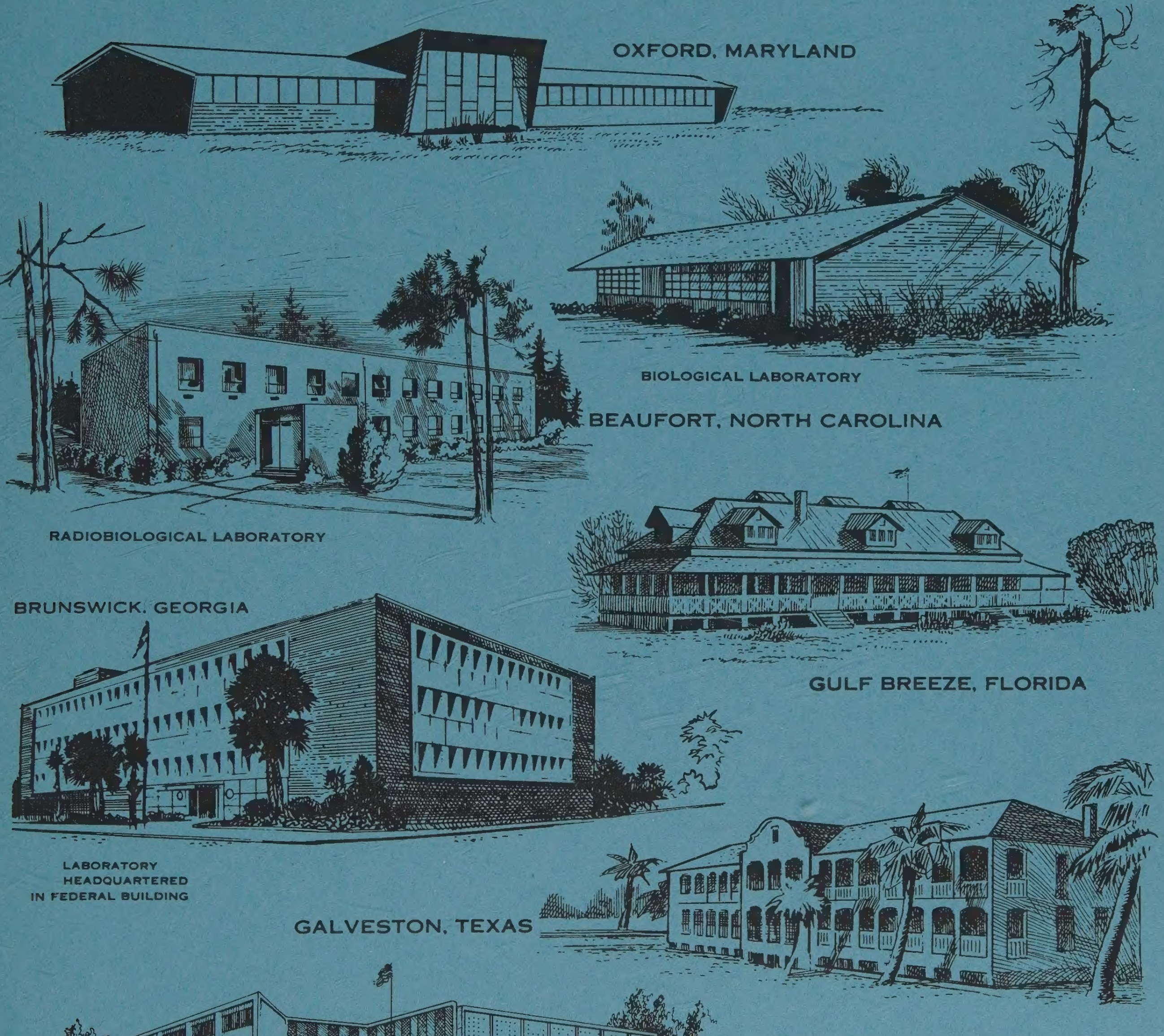

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